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Vertical Migrations and Transport of Larval Fish in a Partially Mixed Estuary[1]

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FORTIER, L., AND W. C. LEGGETT. 1983. Vertical migrations and transport of larval fish in a partially mixed estuary. Can. J. Fish. Aquat. Sci. 40: 1543 – 1555.

The effect of diel or semidiurnal vertical migrations on the horizontal dispersal of fish larvae in a partially mixed estuary, and the external stimuli triggering these migrations, were investigated. The vertical distribution of ichthyoplankton and microzooplankton was estimated at 1-h intervals for 129 h, at a fixed station of the St. Lawrence upper estuary. With increasing length, capelin (*Mallotus villosus*) larvae congregated closer to the surface. This resulted in a length-dependent acceleration of the seaward drift of this species. Larger capelin developed a weak but significant pattern of diel vertical migrations limited to the surface (0–20 m) layer. The average vertical position of early postlarval Atlantic herring (*Clupea harengus harengus*) was close to the depth of null longitudinal velocity. Vertical migrations about this average level followed a semidiurnal cycle which brought the postlarvae toward the surface during flood. This synchronization minimized seaward tidal drift linked to incursions within the surface layer. The large-scale cyclonic circulation prevailing at depth appears responsible for the maintenance of early postlarval herring in the upper estuary. Both the average depth and the semidiurnal migrations of this species were closely related to the vertical distribution of prey.

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L'impact des migrations verticales circadiennes ou semi-diurnes sur la dispersion horizontale des larves de poisson dans un estuaire partiellement mélangé, de même que les stimuli extérieurs déclenchant ces migrations ont été étudiés. La distribution verticale de l'ichtyoplancton et celle du microzooplancton ont été estimées à intervalles d'une heure

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pendant 129 h, à une station fixe de l'estuaire moyen du Saint-laurent. Au cours de leur croissance, les larves de capelan (*Mallotus villosus*) tendent à se regrouper de plus en plus près de la surface. La dérive vers l'aval de cette espèce s'en trouve accélérée de façon proportionnelle à la taille des individus. Les stades plus avancés de capelan développent des migrations verticales nycthémérales de faible amplitude, limitées à la couche de surface (0−20 m). Les stades postlarvaires initiaux de hareng de l'Atlantique (*Clupea harengus harengus*) sont distribués en moyenne à proximité du niveau moyen de vitesse longitudinale nulle. Les migrations verticales autour de cette position moyenne suivent un cycle semi-diurne que amène les organismes vers la surface au flot. Cette synchronisation minimise l'entraînement vers l'aval lié aux incursions dans la couche de surface. La circulation résiduelle cyclonique qui prévaut en profondeur semble responsable du maintien des stades postlarvaires initiaux de hareng dans l'estuaire moyen. La position verticale moyenne, de même que les migrations semi-diurnes de cette espèce sont intimement liées à la distribution verticale de ses proies.

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PLANKTONIC larvae of several species of fish and benthic invertebrates are retained within estuaries against the prevailing seaward circulation (see Bousfield 1955 and Weinstein et al. 1980 for reviews). Because estuaries are characterized by high primary and secondary productivity, an adaptive value has been attributed to this transport strategy which would provide the vulnerable larval stages with adequate food supply (e.g. Pearcy 1962; Dovel 1971). Iles and Sinclair (1982) suggested, in addition, that the retention of fish larvae within a limited area "may be crucial in allowing the aggregation of surviving individuals into schools." It has been further hypothesized that annual fluctuations in the circulation of estuaries or other coastal systems could influence recruitment to fisheries by modifying the extent of larval transport toward retention areas (Pearcy 1962; Pearcy and Richards 1962; Turner and Chadwick 1972; Parent and Brunel 1976; Nelson et al. 1977), or altering the integrity of the retention areas themselves (Iles and Sinclair 1982). In support of these hypotheses, significant correlations have been reported between river discharge during larval drift and subsequent year-class strength (Turner and Chadwick 1972; Sutcliffe 1973; Stevens 1977). A better understanding of the response of larval stages to estuarine circulation is necessary to elucidate and ultimately predict its effect on larval survival (Graham et al. 1972; Parent and Brunel 1976; Fortier and Leggett 1982).

The penetration and maintenance of a cohort of larvae within a definite coastal area can be achieved by the passive occupation of adequate residual currents or the active utilization of tidal circulation (Bousfield 1955; Graham and Boyar 1965). The selection by the adults of spawning grounds from which the larvae emerge directly in the landward residual circulation is well documented (Tibbo et al. 1958; Pearcy and Richards 1962; Iles 1971; Wallace 1975; Able 1978; Courtois et al. 1982). In two-layer circulations, such as partially mixed estuaries, it has been demonstrated that the release and passive maintenance of the newly hatched larvae in the deep countercurrent resulted in the landward penetration and retention of the earliest stages of fish (Pearcy 1962; Melville-Smith et al. 1981; Fortier and Leggett 1982).

With increasing size, the swimming ability of most species increases rapidly and the larvae develop the capacity to control their vertical position (Colton et al. 1961; Pearcy 1962; Miller et al. 1963; Wood 1971; Selivertov 1974; Sjoblom and Parmanne 1978; Smith et al. 1978). Some authors have suggested that in tidally energetic areas, post-larval stages synchronize their vertical migrations with circulation in such a way as to control their longitudinal or lateral transport (Iles 1971; Graham and Davis 1971; Dovel 1971). Rogers (1940) postulated that negatively phototropic rainbow smelt (*Osmerus mordax*) larvae spent more time in the deep inflowing layer of the St. John estuary because daylight is of longer duration than darkness in summer. Graham (1972) suggested that Atlantic herring (*Clupea harengus harengus*) larvae were maintained in the Sheepscot estuary by moving upward upon reaching the limit of their landward penetration with the deep countercurrent, then seaward in the net surface flow, and finally descending again in the landward residual flow. In shallow estuaries, Weinstein et al. (1980) proposed that flounder (*Paralichthys* spp.) postlarvae performed a saltatory landward progression by moving up on flood and seeking boundary layers near the bottom on ebb. A similar mechanism was invoked to explain the lateral penetration of fish larvae into tidal marshes (Lewis and Mann 1971; Weinstein et al. 1980). In deep estuaries, the efficiency of such migrations in favoring the retention of fish larvae is still conjectural. A clear picture of the interaction between diel or semidiurnal vertical migrations of fish larvae and tidal circulation is not available for these systems.

In the St. Lawrence estuary, the newly hatched larvae of the two dominant species of commercial fish respond differently to the two-layer residual circulation. Capelin (*Mallotus villosus*) spawn on both shores of the upper estuary (Parent and Brunel 1976) and after emergence from tidal flats and beaches, the larvae are flushed out of the upper estuary (Jacquaz et al. 1977), toward the most productive zones of the lower estuary (DeLafontaine et al. 1981). Atlantic herring spawn demersally in the vicinity of Iles Verte (Fig. 1). After emergence, the larvae are first carried landward and then retained in the upper reaches (Able 1978), where zooplankton concentrations are relatively high (Bousfield et al. 1975; Gagnon and Lacroix 1981). This opposite response of the dominant species to circulation allows a comparative approach to the study of the mechanisms controlling the

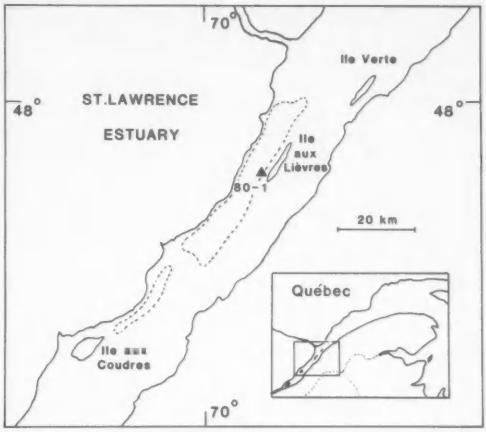

FIG. 1. Sampling location in the St. Lawrence estuary. The broken line represents the 50-m isobath which roughly delineates the North Channel.

longitudinal positioning of fish larvae in two-layer circulations. We have previously demonstrated that the difference in the geographical fate of the initially passive stages of capelin and herring is due to a difference in the average vertical position of the two species (Fortier and Leggett 1982).

In this study, our objective was to assess the impact, on the horizontal dispersal of the larvae, of the interaction between tidal circulation and active vertical migrations which develop later in the early life history of capelin and herring. We also investigated the external stimuli which are potentially triggering these vertical migrations.

Material and Methods

AREA STUDIED AND SAMPLING

The upper region of the St. Lawrence estuary (Fig. 1) is partially mixed (Muir 1980). In early summer, the vertical gradient of salinity is about 10‰ from surface to bottom. In June 1980, time series of larval fish and microzooplankton vertical distribution were obtained at station 80-1 (Fig. 1). Maximum depth at high tide was 51 m. Abundance was estimated for the 0 to 10-, 10 to 20-, and 20 to 40-m-depth strata.

The initial sampling design called for ichthyoplankton and large zooplankters to be collected with a 0.5-m bongo sampler equipped with opening and closing devices, flowmeters, a time-depth recorder, and fitted with 0.510-mm and 0.151-mm mesh nets. Samples were taken every 3 h, at a towing speed of about 6.5 km/h (3.5 knots), from a 21-m ship circling a 47-m mothership anchored on the station. Microzooplankton was simultaneously sampled from the same depth-intervals, at the bow of the mothership, with a 0.5-m standard net (0.080-mm mesh) also equipped with opening and closing devices, a flowmeter, and a time-depth recorder. The standard net was repeatedly moved up and down at a speed of 0.5 m/s within the limits of the depth-stratum sampled. With tidal current acting as the main filtration force, this resulted in a multiple oblique pathway through the desired depth-interval.

This initial sampling regime was maintained for 63 h, until mechanical failure rendered the satellite ship nonoperational. From this moment, the sampling interval on the mothership was decreased to 1 h. The time series thus consisted of a first 63-h series where samples were collected at a 3-h interval with both bongo and standard nets and a second 129-h series taken hourly with the standard net.

Temperature, conductivity, speed, and direction of the current were recorded at 2-min intervals using Aanderaa current meters. Three meters were suspended from the side of the mothership at depths of 3, 10, and 20 m. Three additional instruments were moored within 300 m of the station at depths of 30, 40, and 50 m. Hourly profiles from surface to bottom, at depth-intervals of 5 m, were obtained with a 7th meter.

All plankton samples were preserved in 4% formalin. Larval herring were completely sorted. Sixty-five of the 590 samples contained excessive numbers of capelin larvae and were subsampled with a Fulsom partitioner. From each sample, a maximum of 30 larvae of each species were randomly selected and measured to the nearest 0.04 mm using the photographic technique described by Zwanenburg (1982).

Microzooplankton was enumerated with a model TaII Coulter counter for the following spherical-diameter intervals: 64–80, 80–102, 102–128, 128–160, 160–204, 204–256, 256–320, 320–408, 408–512, and 512–1024 μm.

ANALYSIS

This report is concerned primarily with the detailed analysis of the second section of the time series (hourly collections). Collections made at 3-h intervals with both bongo and standard nets at the beginning of the sampling session were used to assess the efficiency of the standard net. Whenever possible, these collections were included in the analysis to increase statistical reliability.

Short-term variations in the vertical distribution of a species were represented by the fluctuations in the depth of the center of mass of the distribution, Z_{cm}:

$$Z_{cm} = \sum_{i=1}^{3} p_i Z_i$$

where p_i is the proportion of larvae in the ith depth-interval and Z_i is the average depth of the ith stratum.

Autocorrelation and cross-correlation analyses require that the samples be taken at equal intervals in time and, hence, were applied to the hourly section of the time series only. The critical thresholds presented on the correlograms were computed according to Cox and Lewis (1966).

Whenever heteroscedasticity or departure from normality were important, nonparametric tests were used, except in the case of correlation analysis for which the data were transformed [$\log(x + 1)$], when necessary, to avoid the higher computer costs associated with rank-correlation analyses.

TABLE 1. Average density (number/100 m^3) of capelin and Atlantic herring larvae from bongo and standard net collections, by depth-stratum (m). Comparisons are based on samples collected simultaneously by the two gears (n = 17). The ratio of bongo to standard net estimates and the probability of observing a larger difference are given (t-test on the mean of the log-transformed data).

		Capelin				Herring			
		0–10	10–20	20–40	0–40	0–10	10–20	20–40	0–40
Bongo	$\bar{x}$	1342.2	430.8	69.3	614.1	26.1	111.8	72.9	71.7
	SD	1244.7	504.6	117.7	410.3	32.7	94.6	91.3	52.2
Standard net	$\bar{x}$	1579.2	705.2	130.2	804.9	60.0	60.9	38.3	53.0
	SD	761.9	1026.7	335.1	574.4	61.4	62.3	54.1	49.6
Ratio		0.85	0.61	0.53	0.76	0.44	1.84	1.90	1.35
P		0.51	0.34	0.49	0.27	0.06	0.07	0.19	0.29

Results

Efficiency of the Standard Net

The relative efficiency of the tide-strained standard net and the towed bongo sampler was assessed by comparing the number and size of fish larvae captured by the two gears during the first section of the time series. In general, estimates of larval abundance from the two samplers did not differ significantly (Table 1). The standard net yielded a higher estimate of herring density for the 0- to 10-m stratum but a lower estimate for the 10- to 20-m stratum. The length-distribution of larvae caught by the standard and bongo nets differed significantly (Kolmogorov–Smirnov test; capelin, $D_{max} = 0.213$, $P < 0.001$; herring, $D_{max} = 0.074$, $P = 0.03$). Larger larvae appeared to be undersampled by the bongo net (Fig. 2a, b, c, and d), and the average length of both species was slightly but significantly larger in the standard net collections (capelin, $P < 0.001$; herring, $P = 0.03$). We conclude that estimates of larval fish abundance and length-distribution from the tide-strained standard net compared well with those obtained simultaneously with the bongo net which is considered as an adequate sampler of fish larvae smaller than 20 mm (Jacquez et al. 1977; Colton et al. 1980).

The efficiency of the standard net was further tested by comparing the abundance and length-distribution of fish larvae from night and day collections. Catch rates of capelin larvae were not significantly higher at night (Table 2) and the length-distribution of this species did not differ significantly between night and day samples (Kolmogorov–Smirnov test, $D_{max} = 0.022$, $P = 0.28$) (Fig. 2e and f). On average, catches of herring larvae in the top 20 m of the water column were slightly higher at night (Table 2). This could be attributed to gear avoidance in daytime. However, no evidence of daytime avoidance could be found in the comparison of night and day length-distribution (Fig. 2g and h). Thus, the alternative explanation that herring larvae were actually more abundant, on average, in the surface layer at night cannot be rejected.

Tidal current being the main filtration force for standard net collections, the dependence of larval fish catchability on current speed was investigated. No significant positive correlation (r) was found between capelin or herring density (log-transformed) and current speed in any of the three depth-strata (n = 151; $^{**}P < 0.01$):

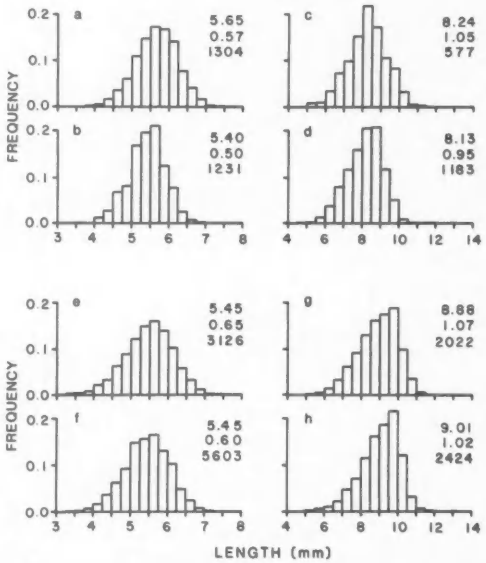

FIG. 2. Top panel: length–frequency distribution of fish larvae for the first section of the time series: (a) capelin, standard net; (b) capelin, bongo net; (c) herring, standard net; (d) herring, bongo net. Bottom panel: length–frequency distribution of fish larvae from standard net collections for the entire time series; (e) capelin, night-collections; (f) capelin, day-collections; (g) herring, night-collections; (h) herring, day-collections. The values on the right-hand side of each histogram correspond, respectively, to the average standard length (mm), the standard deviation, and the number of larvae measured.

	0–10 m	10–20 m	20–40 m
Capelin	−0.32**	−0.01	0.06
Herring	−0.02	−0.04	0.10

The absence of direct dependence of abundance estimates on filtration rate suggests that gear avoidance in slow tidal current was not important.

TABLE 2. Average density (number/100 m^3) of capelin and herring larvae from night (n = 58) and day (n = 93) collections with a standard net, by depth-stratum (m). The ratio of night to day estimates and the probability of observing a larger difference are given (t-test on the means of the log-transformed data).

		Capelin			Herring		
		0–10	10–20	20–40	0–10	10–20	20–40
Night	$\bar{x}$	1654.2	337.9	77.8	63.3	74.5	45.1
	SD	1636.6	593.7	234.6	51.0	66.0	43.3
Day	$\bar{x}$	1350.5	563.6	60.3	46.4	48.9	32.2
	SD	1239.8	774.3	104.8	47.5	39.4	52.5
Ratio		1.22	0.60	1.29	1.36	1.52	1.34
P		0.23	0.05	0.59	0.01	0.01	0.10

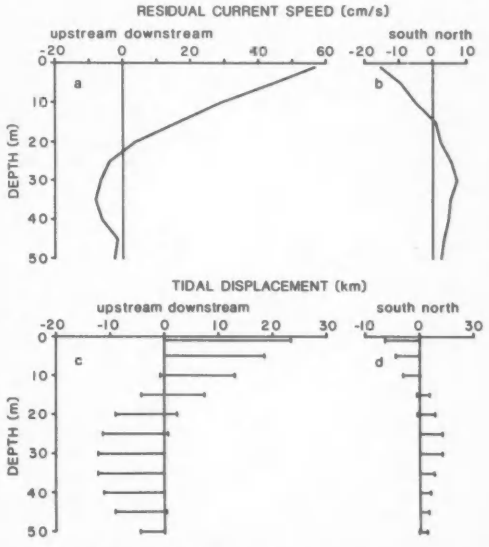

FIG. 3. Vertical profiles of residual circulation and average tidal excursion over the 10 tidal cycles covered by the hourly sampling section of the time series: (a) longitudinal (channel-wise) residual current speed; (b) lateral (cross-channel) residual current speed; (c) average longitudinal tidal excursion; (d) average lateral tidal excursion.

CIRCULATION

The tide-averaged vertical profile of longitudinal (channel-wise) current speed indicated a two-layer residual circulation with a relatively fast seaward net movement in the surface layer and a slow landward countercurrent in the deep layer (Fig. 3a). The depth of null longitudinal velocity was 22.5 m. Residual circulation was southward above the average depth of null lateral velocity (15.0 m) and northward below it (Fig. 3b). The length of the longitudinal tidal excursion varied with depth from 5.0 to 23.4 km and generally decreased from surface to bottom (Fig. 3c). The average cross-channel displacement over one tidal cycle varied with depth from 1.5 to 6.4 km (Fig. 3d).

VERTICAL DISTRIBUTION OF FISH LARVAE

The depth of the center of mass of the vertical distribution (Z_{cm}) was used as an index of short-term vertical displacements. A value of 5.0 m indicates that all the organisms were located in the 0- to 10-m depth-stratum but does not exclude the possibility that their actual average vertical position was above 5 m. Similarly, a value of 30.0 m indicates that all the organisms were captured in the 20- to 40-m depth-stratum but does not exclude that the organisms were, on average, distributed deeper.

Most capelin larvae were captured in the top 20 m of the water column, the highest percentage being found in the first 10 m (Table 3). This pattern became more pronounced with increasing larval length and the average depth of the center of mass of the vertical distribution (Z_{cm}) decreased significantly with increasing size (Wilson's nonparametric ANOVA: $\chi^2 = 77.8$, $P < 0.001$) (Table 3).

The (Z_{cm}) of capelin smaller than 5.0 mm was more variable than that of other length-categories ($F > 4.9$, $P < 0.001$, Table 3) (Fig. 4). With increasing length, capelin larvae became more concentrated within the 0- to 10-m stratum at night and fluctuations in their average vertical position assumed a diel character, the larvae being found closer to the surface in twilight and at night (Fig. 4). The autocorrelation on the (Z_{cm}) of capelin larvae larger than 6.0 mm indicated a weak but significant cycle of 24 h (Fig. 5).

Herring larvae of all lengths were more uniformly distributed over the water column than were capelin larvae (Table 3). The average depth of the center of mass of the distribution (Z_{cm}) decreased significantly with increasing size ($\chi^2 = 11.8$, $P = 0.01$); however, the decrease was less pronounced in herring relative to capelin (Table 3).

Short-term fluctuations in the Z_{cm} of the different length-categories of herring were extremely noisy (Fig. 4). The estimation of Z_{cm} becomes highly variable when the number of organisms considered is small. A significant portion of this noise was probably due to the smaller number of herring larvae sampled relative to capelin (Table 2) and hence the smaller number present in each length-category. Variations in

TABLE 3. Average percentage of total abundance in each depth-stratum for each larval fish length-category (mm) and microzooplankton spherical diameter-category (μm). The average depth of the center of mass of the vertical distribution (Z_{cm}) and the associated coefficient of variation (CV) are also given (n = 151).

	Capelin				Herring				Microzooplankton			
	<5.0	5.0–5.5	5.5–6.0	>6.0	<8.0	8.0–9.0	9.0–10.0	>10.0	64–128	128–256	256–512	512–1024
0–10 m	54.9	72.1	79.9	80.8	32.8	32.8	35.3	47.2	38.4	32.8	30.6	23.9
10–20 m	34.7	24.4	17.7	16.6	38.1	42.5	39.6	34.0	28.4	43.7	35.9	30.7
20–40 m	10.4	3.5	2.3	2.6	29.1	24.7	25.1	18.8	33.2	23.6	33.5	45.4
Z_{cm} (m)	11.1	8.3	7.4	7.1	16.4	15.4	15.0	13.3	16.2	14.2	17.0	19.4
CV(%)	47.0	35.1	32.0	30.3	42.7	35.3	37.2	49.0	22.0	23.5	28.1	28.9

the Z_{cm} of the whole population of herring were more stable (CV = 22.0%) and the autocorrelation function indicated a significant cycle of 12.5 h (Fig. 5). On average, herring larvae were positioned deeper in the water column during ebb when longitudinal transport was seaward, and closer to the surface during flood when longitudinal transport was landward (Fig. 6a and b). The cross-correlation function between the Z_{cm} of herring larvae and the average longitudinal current speed in the 10- to 20-m depth-stratum revealed that the variables were in phase and significantly correlated (Fig. 7). Maximum depth in the distribution of the larvae corresponded precisely with maximum seaward transport whereas minimum depth corresponded with maximum landward transport (Fig. 6a and b, Fig. 7).

VERTICAL DISTRIBUTION AND TIDAL MIXING

The Richardson number ($\hat{R}i$), an index of vertical mixing, was estimated for the 3- to 40-m depth-interval (Fortier and Legendre 1979). High values of $\hat{R}i$ indicate a stable water column. The transition from laminar flow (stability) to turbulent flow (mixing) occurs in theory at a critical value of $\hat{R}i = 0.25$. In estuaries, this transition is likely to take place at higher values because of the nonuniformity of flow (Dyer 1973, p. 20). Fortier and Legendre (1979) considered that values smaller than 3, as calculated from current meter data similar to those used in the present study, were indicative of a potentially destabilized water column. Short-term fluctuations in the Richardson number followed a 12.5-h tidal cycle (Fig. 6c). The water column was stable during flood ($\hat{R}i$ large) and potentially destabilized during ebb ($\hat{R}i$ small).

No significant relationship existed between the fluctuations in the average vertical position of capelin larvae of any length-category and potential vertical mixing (cross-correlation analysis: $r_{max} = 0.112$, $P > 0.21$). Herring larvae were distributed deeper during potential instability and closer to the surface when the water column was stable (Fig. 6a and c). The cross-correlation function between the Z_{cm} of larval herring and $\hat{R}i$ confirmed that maximum depth (large Z_{cm}) corresponded to minimum stability and that the fluctuations of the two variables were significantly correlated (Fig. 7).

The variance(s) between the respective percentages of total abundance found in each depth-stratum at a given sampling hour was computed as a measure of the vertical dispersion of the larvae:

$$s = \frac{1}{3}\sum_{i=1}^{3}(p_i - \bar{p})^2$$

where p_i is the percentage of larvae found in stratum i, and $\bar{p}$ is the average percentage of larvae per stratum. The value of s is minimum when the larvae are evenly distributed in the three strata sampled (maximum physical dispersion of the larvae over the water column) and maximum when all the larvae are concentrated in the same stratum (minimum vertical dispersion). Short-term fluctuations in the vertical dispersion of capelin larvae smaller than 5.0 mm were correlated with the index of stratification ($\Delta\sigma_t/\Delta z$) but were independent of the index of tidal mixing ($\hat{R}i$) (Table 4). Fluctuations in the dispersion of capelin larvae larger than 5.0 mm followed a

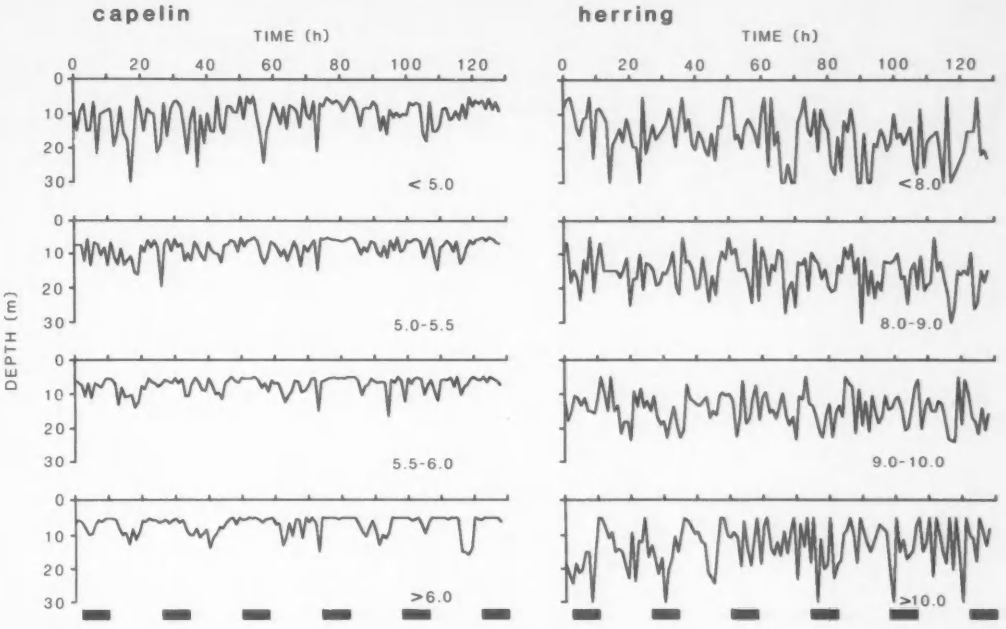

FIG. 4. Time series of larval capelin and larval herring average vertical position (Z_{cm}), by size-category (mm). Heavy horizontal bars indicate darkness.

24-h cycle and did not correlate with either tidal mixing or stratification (Table 4). The variance between the three strata was maximum at night when the larvae concentrated in the surface layer (Fig. 4). Fluctuations in the vertical dispersion of herring larvae followed no precise pattern and did not correlate with tidal mixing or stratification (Table 4).

VERTICAL DISTRIBUTION OF MICROZOOPLANKTON

An examination of the covariability in the abundance of the 10 size-categories of microzooplankton enumerated indicated that the organisms could be grouped into four wider size-categories (64−128, 128−256, 256−512 and 512−1024 μm) without significant loss of information. The smallest size-category (64−128 μm) was numerically dominated by copepod nauplii. The 128- to 256-μm category consisted primarily of copepod nauplii and polychaete larvae. The largest size-categories (256−512 and 512−1024 μm) were represented by copepodid stages. The specific composition and size-frequency distribution of microzooplankton is discussed in detail in Fortier and Leggett (1983).

On average, microzooplankton were quite evenly distributed among the three depth-strata sampled (Table 3). The largest size-categories tended to be positioned deeper in the water column (Table 3). The vertical position (Z_{cm}) of nauplii (64- to 128-μm size-category) was related to the phase of the tide, being deepest during ebb (Fig. 8a). The fluctuations in the Z_{cm} of the 128- to 256-μm size-category

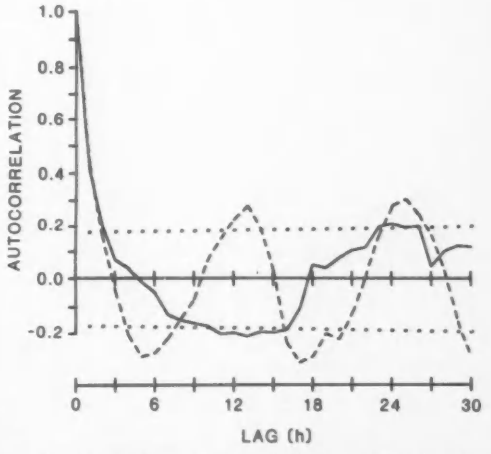

FIG. 5. Autocorrelation function of the time series of average vertical position (Z_{cm}) for capelin >6.0 mm (—) and total herring population (- - -). Dotted lines correspond to the 5% significance thresholds.

were less regular (Fig. 8b). The vertical position of copepodid stages (256- to 512-μm size-category) followed a circadian cycle and was deepest in the water column at night (Fig. 8c).

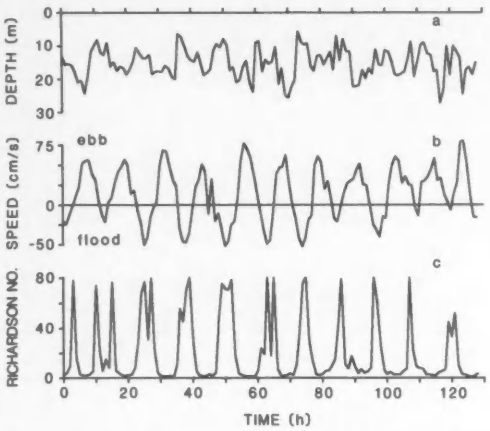

FIG. 6. Time series of (a) average vertical position of herring larvae (total population), (b) average longitudinal current speed in the 10- to 20-m depth-stratum, and (c) estimated Richardson number for the 3- to 30-m depth-interval.

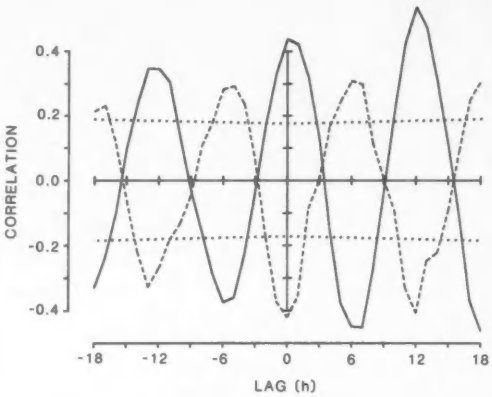

FIG. 7. Cross-correlation function between (1) the average vertical position of herring larvae and the average longitudinal current speed in the 10- to 20-m depth-stratum (—) and (2) the average vertical position of herring larvae and the Richardson number estimated for the 3- to 30-m depth-interval (- - -).

The autocorrelation function of the Z_{cm} of these size-categories confirmed that the patterns of variations described above were statistically significant (Fig. 9). The number of organisms in the 512- to 1024-μm size-category was too small to yield a reliable estimate of short-term fluctuations in vertical position.

COVARIABILITY IN THE VERTICAL DISTRIBUTION OF LARVAL FISH AND MICROZOOPLANKTON

No significant positive correlation was found between the vertical position of capelin larvae and the vertical position of microzooplankton (Table 5). The diel vertical migrations of this species (Fig. 4) were negatively correlated (Table 5) to the diel vertical migrations of the 256- to 512-μm size-category of microzooplankton (Fig. 9c).

The vertical position of herring larvae smaller than 8.0 mm did not correlate with the vertical position of microzooplankton (Table 5). The vertical displacements of herring larvae larger than 8.0 mm, however, were positively and significantly correlated to the vertical displacements of microzooplankton (Table 5). In general, the correlation increased with increasing herring length but decreased with increasing microzooplankton size. Although the time series of Z_{cm} for individual length-categories of larval herring were noisy, the fluctuations nevertheless matched the fluctuations in the Z_{cm} of microzooplankton (Fig. 10). The positions of the two taxa in the water column also coincided (Fig. 10).

Discussion

CIRCULATION

The general circulation in the upper St. Lawrence estuary is cyclonic with a net penetration of water in the North Channel (Fig. 1) and a net extrusion along the south shore (d'Anglejan and Smith 1973). At station 80-1 (Fig. 1), depth-integrated longitudinal transport was seaward during the sampling session (Fig. 4a). The two-layer longitudinal circulation, characterized by a strong seaward residual flow in the surface layer and a sluggish landward countercurrent in the deep layer (Fig. 4a), corresponded to the pattern described by d'Anglejan and Smith (1973). The length of the longitudinal tidal excursion (Fig. 4c) agreed well with values calculated by Gagnon and Lacroix (1981). Lateral circulation was also well developed (Fig. 4b and d), implying a significant lateral transport toward the south shore in the surface layer and toward the North Channel in the deep layer.

TABLE 4. Correlation (r) between the index of vertical dissemination of larval fish (variance between the abundances in the three strata) and the indices of vertical mixing ($\hat{R}i$) and stratification (S). Variables were log-transformed (n = 151; $^{**}P < 0.01$; otherwise nonsignificant).

	Capelin					Herring				
	<5.0	5.0–5.5	5.5–6.0	>6.0	Total	<8.0	8.0–9.0	9.0–10.0	>10.0	Total
$\hat{R}i$	−0.04	0.03	0.05	−0.09	0.06	0.08	0.06	0.02	0.04	0.13
S	0.29**	0.02	0.01	−0.01	−0.05	0.12	0.04	−0.14	0.10	0.04

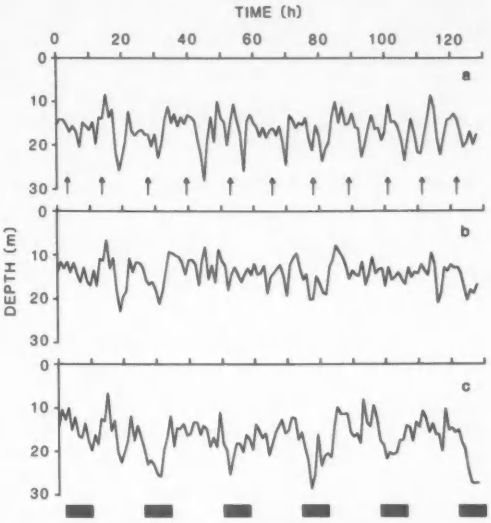

FIG. 8. Time series of microzooplankton average vertical position (Z_{cm}) by size-category: (a) 64−128 μm; (b) 128−256 μm; (c) 256−512 μm. Arrows indicate slack water of high tide. Heavy horizontal bars indicate darkness.

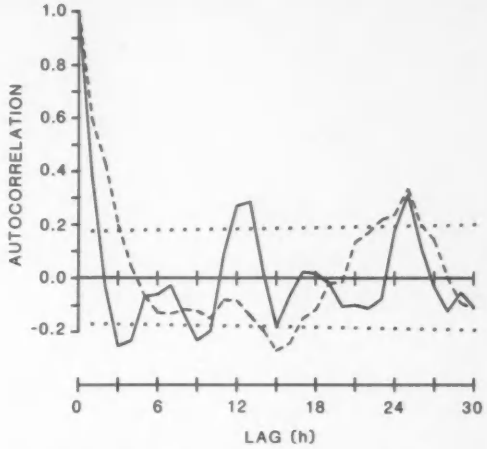

FIG. 9. Autocorrelation function of the time series of microzooplankton average vertical position (Z_{cm}): 64−128 μm, (—); 256−512 μm, (---).

VERTICAL DISTRIBUTION AND DISPERSAL OF FISH LARVAE

Mallotus villosus — We have previously shown that large-scale spatial variations in the vertical distribution of newly hatched larvae (average length of 4.77 mm) reflected the progressive vertical mixing of the surface layer from upstream to downstream (Fortier and Leggett 1982). The vertical dissemination of newly hatched (<5.0 mm) capelin sampled in the present study was significantly correlated with the stratification of the water column which represents the cumulative effects of previous mixing. No relationship, however, could be established between short-term fluctuations in the vertical dispersion of small capelin larvae and the Richardson number ($\hat{R}i$) which is an index of the stability of the water column at the time of sampling. We believe that our sampling resolution on the vertical axis continues to be too coarse to detect the response of the earliest passive stages to the turbulence induced by tidal mixing.

With increasing size, capelin larvae moved closer to the surface in twilight and at night. These nycthemeral migrations were limited to the top 20 m of the water column and hence were not detected by Jacquaz et al. (1977) who used a sampling procedure which integrated this depth-stratum. Working with the assumption that capelin larvae larger than 5 mm did not perform active vertical migration, we predicted (Fortier and Leggett 1982) that the dispersal of these larger larvae, like the dispersal of capelin larvae smaller than 5.0 mm, would be passive. The results of the present study show that assumption to be false. In addition to diel vertical migrations, capelin larvae larger than 5 mm also exhibit a length-dependent tendency to occur closer to the surface. This tendency, coupled with the inverse linear relationship between the intensity of seaward transport and depth in the surface layer (Fig. 4a), caused the rate of seaward transport of capelin larvae to increase with length. The adoption of a shallower average depth with length and the vertical migrations performed by larger larvae along the vertical gradient of longitudinal current speed, both influenced their rate of longitudinal transport. The horizontal dispersal of capelin larvae larger than 5 mm cannot, therefore, be considered purely passive as was previously proposed (Fortier and Leggett 1982). However, as these migrations are of small amplitude and limited to the surface layer, the dispersal of larval capelin in the lower estuary should

TABLE 5. Correlation (r) between the depth of the center of mass of larval fish vertical distribution (Z_{cm}) and that of microzooplankton by size-category (n = 151; *P < 0.05; **P < 0.01; otherwise nonsignificant).

	Capelin				Herring			
	<5.0	5.0−5.5	5.5−6.0	>6.0	<8.0	8.0−9.0	9.0−10.0	>10.0
64−128	−0.07	0.09	0.08	0.02	0.09	0.21**	0.28**	0.24**
128−256	−0.23**	−0.06	−0.08	−0.03	0.07	0.18*	0.37**	0.26**
256−512	−0.18*	−0.17*	−0.22**	−0.25**	0.00	0.04	0.16*	0.19*
512−1024	0.00	0.08	0.11	0.02	0.06	−0.06	−0.01	−0.07

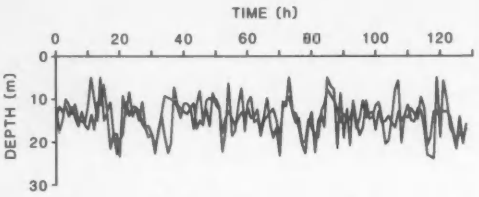

FIG. 10. Time series of the average vertical position (Z_{cm}) of herring larvae (9- to 10-mm length-category) and microzooplankton (128- to 256-μm size-category).

nevertheless approximate the dispersal of freshwater.

Clupea harengus harengus — Our estimate of the average depth of the population of early postlarval herring was 15.2 m. At this depth, the longitudinal residual transport, averaged over 10 tidal cycles, was seaward and relatively important (16.6 cm/s or 7.5 km/tidal cycle, Fig. 4a), suggesting that the population of postlarvae was drifting out of the estuary. However, short-term fluctuations around this average depth of 15.2 m followed a semidiurnal cycle (Fig. 8) that brought the postlarvae to their deepest position when seaward transport in the surface layer was maximum and to their shallowest position when seaward transport in the surface layers was minimal or had reversed to become landward (Fig. 7). A priori, this behavior would appear to represent an adaptation to reduce seaward entrainment by avoiding the stronger surface ebb. The efficiency of this mechanism was assessed by comparing the residual longitudinal drift of the migrating larvae to the longitudinal drift of a static, nonmigrating, population situated at the same average vertical position (15.2 m). The longitudinal displacements of the migrating population were estimated by interpolating from current meter profiles, the longitudinal current speed at the average depth of distribution of the larvae for each hourly collection. These values were then averaged over the 10 complete tidal cycles covered by the time series, to obtain finally a residual longitudinal drift of 10.7 km/tidal cycle. This value is 1.4 times larger than the 7.5 km/tidal cycle calculated earlier for a nonmigrating population. Thus, even if synchronized with the occurrence of minimal seaward transport in the upper stratum, semidiurnal migrations of early postlarvae toward the surface result in an acceleration of seaward drift and cannot, therefore, explain the landward penetration of this species. The timing between upward movements and minimal surface ebb may nevertheless represent an adaptation to minimize seaward drift caused by mandatory feeding-incursions in the seaward-flowing surface layer, and, as such, may contribute indirectly to the retention of the species within the estuary.

The bias in the estimation of Z_{cm} caused by the nonsampling of the deepest 10 m of the water column is believed to be negligible for capelin larvae which were seldom found below 20 m. It is probable, however, that the Z_{cm} of herring larvae was underestimated as this species was apparently distributed over the entire water column (Table 3). Studies in which the near-bottom layer was sampled indicate that postlarval herring span the whole depth range with no tendency to occur in greater number near the bottom (Bridger 1958; Wood 1971; Schnack 1972; Selivertov 1974). If we assume the same concentration of herring larvae in the 40- to 50-m stratum as in the contiguous 20- to 40-m stratum, then the estimation of the average vertical position of this species becomes 19.5 m. At this depth, residual longitudinal transport is seaward at a rate of 4.7 cm/s or 2.12 km/tidal cycle (Fig. 3a). Residual lateral transport, on the other hand, is toward the north shore at a rate of 2.1 cm/s or 0.95 km/tidal cycle (Fig. 3b). Thus, on average, the population of larval herring drifted slowly toward the North Channel (Fig. 1). In the North Channel, newly hatched herring (average standard length of 7.3 mm) were confined to the deep, landward-flowing layer, whereas postlarvae (average standard length of 10.9 mm) were positioned, on average, close to the depth of null velocity (Fortier and Leggett 1982). In the present study, the average vertical position of early postlarvae (average standard length of 8.95 mm) was slightly above the depth of null velocity. These observations suggest that landward penetration of the species takes place mainly before yolk resorption, and is possibly limited to the deeper North Channel where the landward component of residual circulation is stronger (d'Anglejan and Smith 1973).

The subsequent retention of postlarval herring within the upper estuary (Able 1978) apparently results from the tendency for this developmental stage to avoid the strong surface ebb, and to maintain an average vertical position close to the level of null velocity, thus reducing net horizontal displacement. In shallow areas of the estuary where depth-integrated residual circulation is seaward (this station), net transport of early postlarvae appears generally seaward with a significant component toward the North Channel. In the deeper North Channel where depth-integrated residual circulation is landward, the net transport of postlarvae is landward (Fortier and Leggett 1982). Thus, early postlarval herring apparently follow the subsurface large-scale cyclonic circulation prevailing in the upper estuary.

The retention of the early larval stages within tidally energetic areas is a trait common to the life history of several herring populations (e.g. Marshall et al. 1937; Tibbo et al. 1958; Graham and Boyar 1965; Graham et al. 1972; Stobo and Iles 1973; Able 1978; Grainger 1980). Iles and Sinclair (1982) have recently proposed that "the number of genetically distinct herring stocks is determined by the number of distinct, geographically stable larval retention areas." Both tidal currents and residual circulation can play a role in the retention of planktonic larvae within these areas (Bousfield 1955; Graham and Boyar 1965). In the St. Lawrence estuary, the timing of the semidiurnal vertical migrations of herring postlarvae certainly represents an adaptation to limit seaward drift. However, the large-scale cyclonic circulation prevailing at depth appears to be the major factor responsible for the retention of larval herring at this developmental stage.

FACTORS CONTROLLING THE VERTICAL MIGRATION

The largest capelin larvae sampled in this study seldom exceeded 7.0 mm in length. The progressive development of nycthemeral migrations is believed to reflect the development of swimming capability. In the turbid upper estuary,

the limited but significant diel migrations performed by larger individuals within the top 20 m of the water column may be triggered by the search for an optimum light intensity. In full daylight, larger capelin larvae were positioned around 10 m, suggesting that the optimum illumination level was situated around that depth in daytime. In the evening, this hypothetical level of optimum illumination will progressively reach the surface where the larvae congregated and maintained themselves in the absence of light stimulus (Fig. 4).

Moksness (1982) reported that 15-d-old capelin larvae reared in a 5-m-deep outdoor basin descended near the bottom in daytime. This behavior was also observed in 5-m-deep enclosures anchored in the natural environment of this species (DeLafontaine and Leggett unpublished data). Capelin larvae also performed nycthemeral migrations of limited amplitude (5−10 m) in a coastal embayment of eastern Newfoundland (Taggart and Leggett unpublished data). Patterns of vertical migration linked to night and day (Smith et al. 1978; Sjoblom and Parmanne 1978; Weinstein et al. 1979; Kendall and Naplin 1981; Sameoto 1982) or even within-day (Bridger 1958; Wood 1971; Schnack 1972) variations in light intensity have been described for the larval stages of several other species of fish.

The observations by Bjørke (1976) that capelin larvae start feeding at sunrise and stop feeding at nightfall suggests that they are visual feeders. The position of this species in the water column was, on average, well above the vertical position of nauplii or copepodids (Table 3). However, the diel migrations of the larger length-category (>6.0 mm) of capelin larvae brought them deeper in the water column in daytime (Fig. 4), when copepodids were at their highest position (Fig. 8). As a result, the overlap in the vertical distribution of the two taxa was maximum when light intensity was maximum. Feeding rates of capelin larvae smaller than 7.0 mm in the upper St. Lawrence estuary are rather low and copepodid stages are not yet part of their diet (Courtois and Dodson unpublished data). Thus diel vertical migrations at this stage of development cannot be related directly to feeding activity but may represent a precursor of the future feeding behavior of larger individuals. This hypothesis requires verification by an investigation of the relationship between feeding rate, light-availability, and vertical migrations of the larvae at later developmental stages.

Variations in the vertical position of herring larvae were dominated by a semidiurnal cycle. This observation is in agreement with our earlier findings (Fortier and Leggett 1982) for larvae smaller than 10 mm. The tidal advection past a fixed sampling station, of a static horizontal gradient in vertical distribution, would produce apparent semidiurnal cyclic changes in the vertical position of the larvae. Fluctuations in vertical position induced by this phenomenon would be symmetrical about slack water of high or low tide (Gagnon and Lacroix 1981; Cronin 1982). For example, if herring larvae were distributed closer to the surface in the upper reaches of the estuary, the depth of their distribution, as recorded at the sampling station, would progressively decrease during ebb, attain a minimum at slack water of low tide, and then increase again with flood. In the present study, semidiurnal fluctuations in the vertical position of herring larvae were precisely in phase with current speed (Fig. 7) so that the extreme vertical position of this species did not correspond to slack waters but to maximum ebb and maximum flood (Fig. 6a and b). The vertical position of herring larvae sampled in a given water mass was low during ebb, and then high during flood when the same water mass was brought back to the station. We conclude that the fluctuations in the vertical position of herring larvae resulted primarily from active migrations.

In an earlier study, we hypothesized that fluctuations in the vertical distribution of ichthyoplankton could be induced by tidal mixing (Fortier and Leggett 1982). Stabilization and destabilization of the water column will primarily influence the vertical dispersion of weak swimmers. We therefore expected the larvae to be more uniformly distributed over depth during tidal mixing and to reassemble at a preferred level during periods of stability. This expectation was not upheld. No correlation was found between the index of tidal mixing and the index of vertical dispersion of herring larvae. As noted above, this lack of correlation could result from the limited resolution of our sampling on the vertical axis, resulting in a poor estimation of the true dispersion of the organisms over depth.

Intensive vertical mixing may also influence the average vertical position of weak swimmers. For example, surface-dwelling organisms with little swimming ability will be found, on average, deeper in the water column during vertical mixing. The average vertical position of herring larvae was deeper during periods of potential instability. A priori, this suggests that herring could not resist tidal mixing. However, at an average size of 9 mm, herring larvae were fairly developed and probably capable of resisting turbulent vertical diffusion induced by tidal mixing.

An alternative explanation for the relation between tidal mixing and the vertical position of herring larvae, is that the latter followed copepod nauplii which are more likely to be vulnerable to tidal mixing. Our results indicate that both the average level and the fluctuations in the vertical distribution of herring larvae and copepod nauplii coincided (Table 4 and Fig. 10). As copepods metamorphosed from nauplii to copepodids and increased their swimming power, the rhythm of their vertical displacements changed from tidal to circadian (Fig. 8). Interestingly, we previously observed an identical length-dependent transition in the character of larval herring vertical migrations in the St. Lawrence estuary (Fortier and Leggett 1982). Those observations indicated that the fluctuations in the vertical position of herring larvae smaller than 10 mm were dominated by a 12.5-h tidal cycle, whereas herring larvae larger than 10 mm moved from the deep layer toward the surface layer in daytime. We conclude that semidiurnal migrations of feeding herring larvae do not constitute an active response to changes in the nature of tidal flow (Graham 1972), nor a passive response to vertical mixing (Fortier and Leggett 1982), but rather a behavioral response to fluctuations in the vertical distribution of their prey. The initial semidiurnal migration (Fig. 6a) apparently follows the passive response of nauplii to tidal mixing (Fig. 8a). With increasing size, the larval diet includes larger and larger items and herring migrations take a circadian character (Fortier and Leggett 1982) similar to that of copepodid migrations (Fig. 8c). Ellertsen et al. (1981) reported that copepod nauplii

developed diel migrations with increasing size and that the vertical distribution of first feeding cod (*Gadus morhua*) larvae corresponded to the vertical distribution of nauplii in daytime.

A recent review of the literature by Graham and Sampson (1982) revealed a considerable variability in the pattern of vertical migration of herring larvae. In areas less affected by tide, the vertical displacements of first-feeding herring do not follow a tidal cycle. These displacements are known, however, to increase and take a diel character as larval size increases (Wood 1971; Selivertov 1974). In some instances, larger larvae have been reported to concentrate near the surface at night whereas in other instances, the same distribution was observed in daytime (Graham and Sampson 1982). Sjoblom and Parmanne (1978) found that the two behaviors could alternate during the summer. These observations indicate that the light cycle alone cannot explain the various patterns of migration exhibited by this species. Local conditions of turbidity, size-dependent shift in diet, and the vertical displacements of the preferred food items probably all contribute to trigger the migrations.

Newly hatched capelin and herring larvae adopt species-specific transport strategies by emerging and passively remaining either in the surface or deep layer (Fortier and Leggett 1982). During development, the character of vertical displacements progressively shifts from passive to active as swimming capacities develop. Our results indicate that the amplitude and timing of larval fish vertical displacements are adapted to minimize interference with the general transport strategy of each species. The effect of the large-scale circulation remains, however, the central determinant of the horizontal dispersion of the larvae.

Acknowledgments

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Dynamics of An Exploited Population of Lake Whitefish (*Coregonus clupeaformis*) in Lake Huron[1]

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HENDERSON, B. A., J. J. COLLINS, AND J. A. RECKAHN. 1983. Dynamics of an exploited population of lake whitefish (*Coregonus clupeaformis*) in Lake Huron. Can. J. Fish. Aquat. Sci. 40: 1556–1567.

A population of lake whitefish (*Coregonus clupeaformis*) in the waters off eastern Manitoulin Island in Lake Huron was sampled from 1950 to 1982 by an experimental pound net in the outer basin of South Bay. Year-class strength increased markedly from 1947 to 1977; the increase began with the decline of the 1943 year-class. The fork length attained by age 1–3 fish decreased during the study, but no trend was apparent for older fish. Natural mortality of year-classes varied considerably, and was probably related to the abundance of lamprey. The annual exploitation rate increased from 1 to 37% between 1960 and 1977. Year-class strength was not correlated with the thermal regime during spawning and hatching. Recruitment was a function of parental stock size, and there was evidence that survival from the egg to juvenile stage was inversely correlated with parental stock size. Instantaneous growth rates (G) during the 2nd year of growth were inversely related to year-class strength. Growth (G) in the 1st year was positively correlated with estimated surface water temperatures. The sizes attained by ages 2 and 3 were inversely related to total population abundance. Catchability coefficients in 144-mm-mesh gill nets were inversely related to estimated population sizes. An intrinsic mechanism of population regulation is proposed whereby recruitment is a function of parental stock size, juvenile survival is inversely related to stock size, and growth is inversely correlated with population abundance.

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Entre 1950 et 1982, nous avons échantillonné une population de grands corégones (*Coregonus clupeaformis*) dans les eaux du large de l'est de l'île Manitoulin, dans le lac Huron, à l'aide d'une pêcherie fixe tendue dans le bassin extérieur de la baie Sud. L'abondance des classes d'âge a notablement augmenté de 1947 à 1977; cette augmentation a débuté au moment où déclinait l'effectif de la classe d'âge de 1943. La longueur à la fourche atteinte par les poissons d'âge 1 à 3 diminua au cours de l'étude, alors qu'aucune tendance n'a été apparente chez les poissons plus âgés. La mortalité naturelle des classes d'âge accusa de fortes variations, probablement liées à l'abondance des lamproies. Le taux annuel d'exploitation a augmenté, passant de 1 à 37 % entre 1960 et 1977. Nous n'avons pu établir de corrélation entre les effectifs de classes d'âge et le régime thermique au moment de la ponte et de l'éclosion. Le recrutement est fonction de la taille du stock parental, et on a des indications que la survie de l'oeuf au stade de juvénile est en relation inverse avec la taille du stock parental. Les taux instantanés de croissance (G) durant la deuxième année de croissance sont inversement reliés à l'abondance de la classe d'âge. La croissance (G) de première année est en corrélation positive avec les températures de l'eau de surface estimées. Les tailles atteintes par les poissons d'âge 2 et 3 sont en relation inverse avec l'abondance de la population totale. Les coefficients de capturabilité dans des filets maillants à mailles de 144 mm sont en relation inverse avec les effectifs de population estimés. Nous proposons un mécanisme intrinsèque de régulation de population en vertu duquel le recrutement est fonction de la taille du stock parental, la survie des juvéniles en relation inverse de la taille du stock et la croissance également en relation inverse avec l'abondance de la population.

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MANAGEMENT of exploited populations of fish can best be achieved by using methods of harvesting that at least do not impair the natural regulatory mechanisms of the population. Ideally, one should at first comprehend how the population is regulated, and then institute a method of harvest that complements these mechanisms.

The purpose of this study was to describe the population dynamics of a lake whitefish (*Coregonus clupeaformis*) population, and its commercial fishery in Lake Huron, and to assess five hypotheses regarding recruitment, growth, and fishing. These were as follows:

1) Recruitment was related to thermal conditions during spawning and hatching — Christie (1963) suggested that even if a stock–recruitment relationship existed, it would be obscured by a stronger effect of temperature on year-class strength. This hypothesis was assessed by applying the statistical technique used by Christie (1963). The absence of a significant positive correlation between Christie's (1963) index and year-class strength would indicate a rejection of this hypothesis.

2) Recruitment was related to parental stock size — There are at least three general hypotheses about the relationship between stock size and recruitment. First, recruitment is a linear function of the product of parental stock size and fecundity. Second, recruitment is density dependent so that recruitment is higher at lower stock size or year-class strength (Ricker 1958; Beverton and Holt 1957). Third, environmental factors influence stock and recruitment, thus effectively obscuring the underlying relationship between parental stock size and recruitment (cf. Christie 1963). These hypotheses were investigated by comparing the estimated size of the parental stock and egg production with the observed year-class strength. Two possible density-dependent factors affecting recruitment, that is, survival from the egg to age 1 and growth, were investigated. The first hypothesis would be rejected if recruitment was not positively and linearly correlated with parental stock size. The second hypothesis was rejected if there was no evidence of density-dependent factors affecting recruitment. The third hypothesis was rejected if any positive correlation existed between parental stock size and recruitment.

3) Growth was inversely related to population abundance — Healey (1980) concluded that growth in whitefish was enhanced after the population was reduced by exploitation. The implication was that there was competition for resources, alleviated by a reduction in population size. Consequently, recruitment could be partly regulated by variations in growth. Intensively exploited populations would grow faster, mature earlier, and therefore produce more offspring than more dense populations that grow more slowly, mature later, and experience more natural mortality before maturation. This hypothesis was assessed by correlating growth rates in the first 3 yr of growth with year-class strength and total population size. The absence of a negative correlation between growth and either year-class strength or total population was considered to be a rejection of the hypothesis.

4) Growth in the 1st year was related to surface water temperatures — A wealth of information exists describing the effect of water temperature on growth in fish (Brett 1979). Deviation of water temperature from the optimum can result in reduced rates of growth because of changes in activity, feeding, and digestive physiology. This type of environmental factor could theoretically obscure the effect of population size on growth, and therefore, eliminate variations in growth as a mechanism for regulating recruitment. This hypothesis was assessed by comparing instantaneous rates of growth (G) with estimated surface water temperatures. This assessment was obviously not very elegant because only one age-class (0–1) was principally affected by surface water temperatures. Thus, the hypothesis that growth from age 0 to 1 was correlated with water temperature was rejected if there was not a significant positive correlation between (G) and temperature.

5) Catchability coefficients varied inversely with abundance — Usually the catchability coefficient ($q = C \cdot f^{-1} \cdot N^{-1}$, where C = catch, f = nominal fishing effort, and N = fish abundance) is assumed to be constant by fisheries managers, and therefore the catch-per-unit of effort (km of gill net) is linearly related to fish abundance. It is evident that in many cases catchability is inversely related to population size (Peterman and Steer 1981). This hypothesis was rejected if there was not an inverse correlation between catchability and estimated population size.

Data were obtained from whitefish caught in an experimental pound net fished for 33 yr (1950–82) in the outer basin of South Bay (Fig. 1), and from the commercial fishery (1958–82) in the adjacent waters of Lake Huron.

Methods

POPULATION SIZE AND STRUCTURE

Samples of the whitefish population were obtained from an experimental pound net with a crib mesh of 76 mm (stretched measure) which was fished annually (nets lifted every 1–6 d) in 9 m of water at site P-6 (Fig. 1), during June, from 1950 to 1982. The peak of recruitment to the net was at age 3, so that total catch-per-unit of effort (CPUE) for each year was determined by dividing the catch (number of fish older than 2) by the total number of nights that the net was set (effort). The CPUE of each age-class was found by multiplying the total CPUE by the proportion of fish at each age. Year-class strength (YCS) was estimated by summing the CPUE from ages 3 to 15, for each year-class.

GROWTH AND MATURATION

A sample was taken from the catch in the pound net to assess ages, weight (g), fork length (mm), and sexual maturity. At each lift 30–60 fish were dipnetted and retained for detailed measurements, but nearly all were sampled for scales and fork length (624 ± 85, $\bar{x}$ ± SE). The ages of whitefish were obtained by counting annuli (Van Oosten 1923) from scale impressions on acetate slides. In June, there was little or no body or scale growth so that back-calculations could be

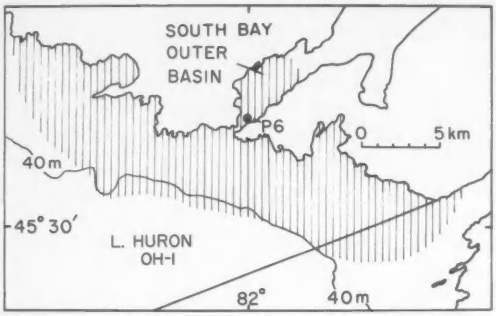

FIG. 1. Location of sampling gear and population defined by recaptures (hatched areas).

made to estimate the size at earlier ages, assuming that the relationship between the longitudinal diameter of the scale and body length was linear (cf. Van Oosten 1923). Measurements were made on scales projected on an Eberbach screen, magnified 45×. Three different age-classes (2, 3, 4) in 1959, 1963, and 1975 were chosen for back-calculations to determine if there was any obvious bias caused by the size selectivity of the sampling or commercial gear, as discussed by Lee (1912). It was concluded that unbiased back-calculations could only be done from age 3 fish. The size of whitefish at hatching (age 0) was assumed to be 12.9 mm (Berlin et al. 1977). Back-calculations of the sizes at ages 1 and 2 were done on 25 randomly selected samples of 3-yr-olds taken each year from 1958 to 1980. The instantaneous growth rates (difference between natural logarithms of fork length from age t to $t+1$) were calculated for the first 3 yr of growth.

Sexual maturity was a subjective assessment of whether or not the fish would spawn in the following autumn, based on the size of the gonad.

Spawning Stock Size, Egg Production, and Survival from Egg to Age 1

Spawning stock size was estimated by multiplying CPUE at age by the proportion mature (dependent upon size) at each age. Egg production was calculated by multiplying the size of the spawning stock of females at each age by the fecundity of females in the age-classes.

$$E_t = \sum_{a=1}^{n} N_{ta} \cdot M_{ta} \cdot W_{ta} \cdot F_{ta}$$

E_t = total egg production of spawning population
N_{ta} = number of females
M_{ta} = proportion mature
W_{ta} = weight (g)
F_{ta} = fecundity (18 eggs/gram of round body weight; Cucin and Regier 1966).

We assumed that the maturation schedule, weight–length relationship, fecundity, and sex ratio (1:1) of the population were constant. The size and CPUE at age from 1950 to 1977 were the only variable factors. Using these data, we estimated the relative size (in units of CPUE) of the spawning stock and egg production from the pound net catch in June; the catch in June (t) provided a minimum estimate of the spawning stock at time ($t-1$).

Having calculated relative egg production, one needed the CPUE at age 1, to estimate the survival from egg to yearling. The CPUE at age 1 was found by extrapolating from the CPUE at age 3, assuming a natural mortality rate of 34% (Cucin and Regier 1966). These calculations were done for the years from 1950 to 1977, for which complete information was available.

Stock Recruitment Analysis

The parameters of the Ricker recruitment curve were estimated from the following equation:

$$\text{Log}_e R/P = \log_e \propto -\beta \cdot P,$$

as described by Ricker (1975). The intercept ($\log_e \propto$) and the slope (β) were used to estimate the parameters ($\propto$, β) of the stock recruitment curve:

$R = \propto \text{Pe}^{-\beta \cdot P}$
R = recruits at age 1
P = number of eggs or spawning females representing parental stock size.

The regression equation:

$$1/R = \propto + \beta/P$$

was used to estimate the parameters ($\propto$, β) of the curve described by Beverton and Holt (1957):

$$R = 1/(\propto + \beta \cdot P).$$

Commercial Catch

Both the catch in kilograms and the effort in kilometres of 114-mm-mesh (stretched measure) gill net were obtained from the commercial fishermen's records (Ontario form CF.1) from 1958 to 1982, for the whitefish caught near South Bay in Statistical District OH-1 (Smith et al. 1961). The duration of the set was not known. Therefore, the commercial CPUE was defined as the catch in kilograms divided by the effort in kilometres of net lifted. The number of fish tagged annually with streamer tags and released from the pound nets varied from zero (1956–57, 1965–69) to 1914, with an average of 829 ± 123. One dollar was paid for each tag which was returned with a description of the date and location of capture.

Population estimates (n = 14) were made from the commercial catch, using a single census Petersen estimate (Chapman 1951) as follows:

$$N = ((M + 1) \cdot (C + 1))/(R + 1),$$

where the number of fish sampled (C) was determined by dividing the weight (kg) of the commercial catch by the average weight of a 4-yr-old (1.18 kg) (the catch consisted mostly of 4-yr-olds), the tagged sample (M) comprised fish (≥4-yr-old) susceptible to the commercial gill net (114 mm), and recaptures (R) were caught within 6 mo of tagging in

TABLE 1. Stock size (egg production and spawning females), year-class strength at age 1, and percentage survival (0−1) (all in units of CPUE). Estimated water temperatures in November and April, as well as the corresponding thermal index.

Year	Year-class strength	Mature females ($t-1$)	Egg production	% survival age 0−1	November °C	April °C	Thermal index
1947					1.277	1.833	−0.366
1948					1.611	5.166	+2.633
1949					5.055	4.944	−1.033
1950	10.01	30.30	58 801	0.017	0.333	0.222	−1.033
1951	4.71	28.25	59 023	0.008	0.777	4.722	+3.023
1952	4.16	10.20	22 447	0.019	−2.333	5.666	+7.077
1953	2.89	3.94	9 072	0.032	2.555	3.000	−0.477
1954	4.29	1.09	2 039	0.210	3.944	3.444	−1.422
1955	24.24	0.43	764	3.170	3.777	6.555	+1.856
1956	12.56	0.55	1 276	0.984	1.166	1.500	−0.588
1957	15.01	1.07	2 671	0.560	2.722	3.833	+0.188
1958	24.03	1.30	2 314	1.060	3.222	4.444	+0.300
1959	30.00	1.16	2 122	1.400	2.777	3.000	−0.699
1960	32.58	2.03	4 147	0.786	0.777	3.166	+1.467
1961	50.02	1.99	3 409	1.467	4.388	3.277	−2.033
1962	18.37	1.44	2 205	0.833	3.000	3.111	−0.811
1963	25.12	2.99	5 085	0.494	2.722	3.611	−0.033
1964	29.02	3.14	4 880	0.595	4.833	3.222	−2.533
1965	38.27	2.56	4 591	0.834	3.444	1.500	−2.866
1966	55.35	1.16	2 001	2.766	1.666	3.444	+0.856
1967	70.50	1.47	2 616	2.695	2.333	2.888	−0.367
1968	43.32	1.93	3 342	1.296	0.000	5.111	+4.189
1969	31.75	2.88	5 079	0.625	1.555	3.611	+1.134
1970	45.57	4.60	8 500	0.536	2.055	2.722	−0.254
1971	12.92	2.84	5 461	0.237	2.666	2.111	−1.477
1972	109.92	3.93	8 473	1.297	2.277	1.000	−2.199
1973	86.00	3.49	7 015	1.226	1.000	3.833	+1.910
1974	81.54	0.57	1 251	6.518	1.777	3.055	+0.356
1975	124.54	3.46	6 789	1.834	2.555	0.944	−2.533
1976	30.97	4.56	7 534	0.411			
1977	195.87	4.31	8 189	2.392			

June. Then these estimates were regressed on the total CPUE in each year, to provide an estimate of the total population in those years when a Petersen estimate was not possible. Catchability coefficients were calculated by dividing the commercial catch (numbers) per kilometre of net by the estimated population.

MORTALITY

The total instantaneous mortality rate (Z) for each year-class was found by regressing the natural logarithm of CPUE on age. The annual conditional fishing mortality rate ($m_i = 1 - e^{-F_i}$) was estimated by calculating the proportion of tagged fish returned by the commercial fishermen at each age by:

$$\sum_{j=2}^{j=10} [\ln(1 - R_{ij}/E_{ij})]/C_i = F_i$$

R_{ij} = number of recaptures from commercial fishery
E_{ij} = number of extant tags
C_i = number of years that the year-class is vulnerable to the fishery
i = year-class
j = age-class.

The number of extant tags was calculated by:

$$[(T_{i-1,j-1}) - (R_{i-1,j-1})] \cdot (1 - n) = E_{ij}$$

T_{ij} = number of tagged fish at the start of the year
R_{ij} = number of tagged fish recaptured by fishery in the year
n = natural mortality rate (assumed to be 34%).

The conditional natural mortality rate was calculated by subtracting the instantaneous rate for fishing from the instantaneous total (e.g. $n = 1 - e^{-(Z-F)}$).

The fishing mortality rates were corrected for a natural mortality rate of tagged fish of 34% (cf. Cucin and Regier 1966). The corrections, for natural mortality and removal by fishermen, were applied to avoid an underestimation of fishing. These estimates of fishing mortality were not corrected for the accidental loss of tags, which was probably less than 3% (Cucin and Regier 1966; Spangler 1970). Our estimates may also have been biased by an increased vulnerability of tagged fish to 114-mm gill net, if streamer tags snagged on the filament, but we had inadequate data to test for this. If tagged fish were more vulnerable, then our estimate of F was exaggerated.

TABLE 2. Maturation schedule of male and female whitefish (1950–73 year-classes) caught in the pound net (June).

		Size (4-cm fork-length interval)										
		20	24	28	32	36	40	44	48	52	56	60
Male	% mature	0.0	9.8	5.1	19.4	51.2	78.1	92.1	94.3	100.0	66.6	
	N	9	51	98	62	260	310	228	70	16	3	
Female	% mature	0.0	2.2	0.0	4.7	21.3	53.5	84.4	92.3	92.3	100.0	100.0
	N	12	92	104	85	211	271	225	91	13	1	1

		Age						
		2	3	4	5	6	7	8
Male	% mature	6.3	46.4	83.9	93.1	98.4	94.1	85.7
	N	(159)	(373)	(311)	(147)	(61)	(51)	(7)
Female	% mature	1.0	15.3	62.4	90.3	98.0	95.1	66.7
	N	(205)	(308)	(346)	(145)	(49)	(41)	(9)

TABLE 3. Regression statistics for Ricker and Beverton–Holt stock–recruitment curves.

Regression variables						
Dependent	Independent	r^2	Slope	Intercept	*F*	Σd^2_{yx}
			Ricker curve			
$\ln R/P$	*P* (eggs)	0.591	−0.0001	−4.3776	40.15162	1.061
$\ln R/P$	*P* (♀♀)	0.571	−0.1723	3.1695	37.01076	1.067
			Beverton–Holt			
$1/R$	$1/P$ (eggs)	0.040	−56.7825	0.0846	0.9531492	0.085
$1/R$	$1/P$ (♀♀)	0.030	−0.0247	0.0816	0.6929016	0.086

In addition to estimating the annual instantaneous rate of fishing on individual year-classes, we also calculated the percentage of extant tags captured (exploitation rate) by the commercial nets each year.

Results and Conclusions

THERMAL REGIME DURING INCUBATION AND YEAR-CLASS STRENGTH

Because Lake Huron whitefish spawn in November and the eggs hatch in late April, annual variations in water temperature for these months could influence spawning and hatching success, and thus year-class strength. We were unable to demonstrate any effect of temperature on year-class strength, by regressing the deviations of YCS on the thermal index (cf. Christie 1963) ($r = -0.32, P > 0.05, n = 29$, Table 1). The formula for the thermal index was:

$$I_{t+1} = (A_{t+1} - \bar{A}) - (N_t - \bar{N})$$

I = thermal index
A_{t+1} = average temperature in April at year $t+1$
N_t = average temperature in November at year t
$\bar{A}$ = average April temperatures over all years
$\bar{N}$ = average November temperatures over all years.

Water temperatures were estimated using the equations described by McCombie (1959). Deviations of year-class strength were also not significantly correlated with either November temperature deviations ($r = +0.12$) or April deviations ($r = -0.33$) (Table 1). Further, when actual rather than estimated water temperatures in Lake Huron were used, we still found no significant correlation ($r = -0.46$, $P > 0.05$, $n = 12$).

PARENTAL STOCK SIZE AND RECRUITMENT

Parental stock sizes were calculated using the maturation schedule (proportion mature $= L^{16}/(41^{16} + L^{16})$; L = fork length (cm), Table 2), sex ratio (1:1; Table 2), and the length–weight relationship ($\ln W = -12.2443 + 3.17303 \ln L$; W(g), L(mm)) derived from this study.

A Ricker stock–recruitment curve was consistent with our data (Tables 1 and 3, Fig. 2). The regression of $\ln R/P$ on potential egg production (P) was significant ($r^2 = 0.591$, $F = 40.15$, $P < 0.001$) and so was the regression of $\ln R/P$ on the number of mature females ($r^2 = 0.571$, $F = 37.01$, $P < 0.001$). The equation describing the relationship between year-class strength at age 1 and potential egg production was:

$$R = 0.01256\, P_e^{-0.0001\, P_e}.$$

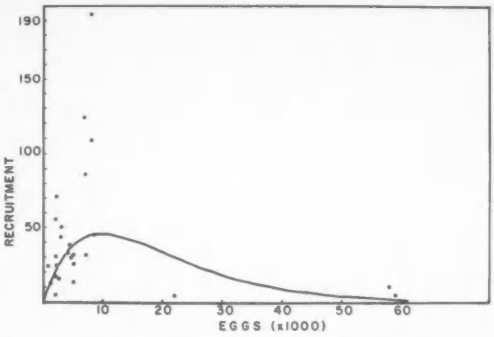

FIG. 2. Relationship between recruitment (relative year-class strength) at age 1 and parental stock size (egg production from estimated CPUE of mature females) from 1950 to 1977.

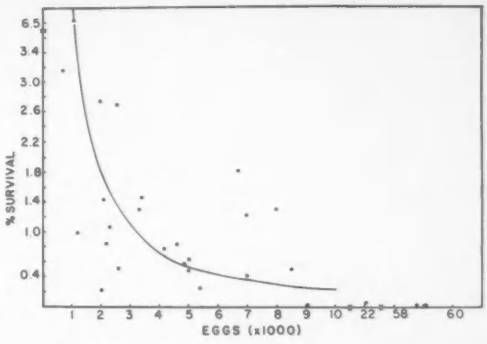

FIG. 3. Percentage survival (egg production/YCS at age 1 × 100) in relation to parental stock size (egg production from estimated CPUE of mature females).

The corresponding equation for year-class strength on the number of mature females was:

$$R = 23.79558\ P_f^{-0.1723\ P_f}.$$

In contrast, the Beverton–Holt recruitment curve, computed by the regressions of $1/R$ on both $1/P$ (eggs) ($r^2 = 0.04$, $F = 0.0846$, $P > 0.05$) and $1/P$ (spawners) ($r^2 = 0.03$, $F = 0.0816$, $P > 0.05$) were not significant. The spawning stock (eggs) needed to produce maximum recruitment was 10 000 ($Pm = 1/\beta$), and the corresponding maximum recruitment was 46.2 ($Rm = \alpha/\beta_e$).

Survival (egg to age 1) was negatively correlated with egg production [$r = -0.78, P < 0.001, y = 28168.9054x^{-1.2766}$ (Table 1, Fig. 3)] and the number of mature females ($r = -0.76, P < 0.001, y = 1.8049x^{-1.2579}$); the reason for using this regression model over either the linear or negative exponential form was that the power curve explained more of the variation.

Year-class Strength, Population Size, and Growth

The CPUE in the pound net declined from 1950 to 1956, with the attrition of the exceptionally large 1943 year-class, and then increased to the present (Fig. 4, Table 4). From 1950 to 1953, the catch was dominated by members of the 1943 year-class. The strength of the year-classes increased sharply since 1947 (Fig. 4), accounting for a large part of the variation in total CPUE.

The regression of 14 population estimates (1958, 1960–64, and 1970–77) on the corresponding CPUE from the pound net was significant ($y = 3445.237 \cdot X + 31647.331, n = 14, F = 6.9733, P < 0.025$). The estimated population size of fish older than 2 decreased from over 370 thousand in 1950 to 37 thousand in the midfifties, and then rose to 530 thousand by 1982 (Table 4).

During the study, the fork lengths (mm) at ages 2 ($r = -0.93$, $P < 0.001$) and 3 ($r = -0.92$, $P < 0.001$) were largest during the late 1950s and thereafter tended to decline, but the sizes at older ages did not change in a consistent way (Table 5). Back-calculated sizes at age showed that fork lengths decreased at age 2 ($r = -0.58, P < 0.001$) but not at age 1 ($r = -0.38, P > 0.05$) for the year-classes from 1955 to 1977 (Table 5).

To assess the hypothesis that growth was inversely correlated with year-class strength, the instantaneous growth rate (G) in length was compared with YCS. These calculations were made with back-calculated sizes at ages 1 and 2. We chose age 3 for back-calculations because by age 3 the whitefish had fully recruited to the pound net, but not fully recruited to the commercial gill nets; the results indicated that the estimated sizes at earlier ages decreased as one back-calculated from older fish, for possibly two different reasons. First, age 2 whitefish did not recruit fully to pound net No. 6 and therefore, the net probably caught the faster growing fish. Second, the age 4 fish had recruited to the commercial nets which removed the faster growing fish, and consequently left behind the slower growing ones.

Growth (G) was negatively correlated with year-class strength in the 2nd year of growth ($r = -0.47, P < 0.05$, Fig. 5); there was no correlation between YCS and growth (G) in the 1st or 3rd year of growth. Growth (G) was not correlated with total population size during the growth periods from ages 0–1, 1–2, 2–3, or 3–5 ($P > 0.05$). Fork lengths attained at ages 2 ($r = -0.55, P < 0.01$) and 3 ($r = -0.47$, $P < 0.01$) were negatively correlated with total CPUE in the pound net.

Temperature and Growth

The hypothesis that growth was correlated with water temperature was investigated by comparing instantaneous growth (G) in the first 3 yr of growth prior to the size-selective action of the commercial gill nets. The number of degree days above 0°C (May–November) was correlated with growth (G) in the first ($r = 0.47, P < 0.05$, Fig. 6), but not during the 2nd or 3rd year of growth ($P > 0.05$).

Catchability Coefficients and Population Size

The commercial CPUE (fish/km) was correlated with the CPUE at P-6 in the same year ($r = 0.79, P < 0.001$). In the

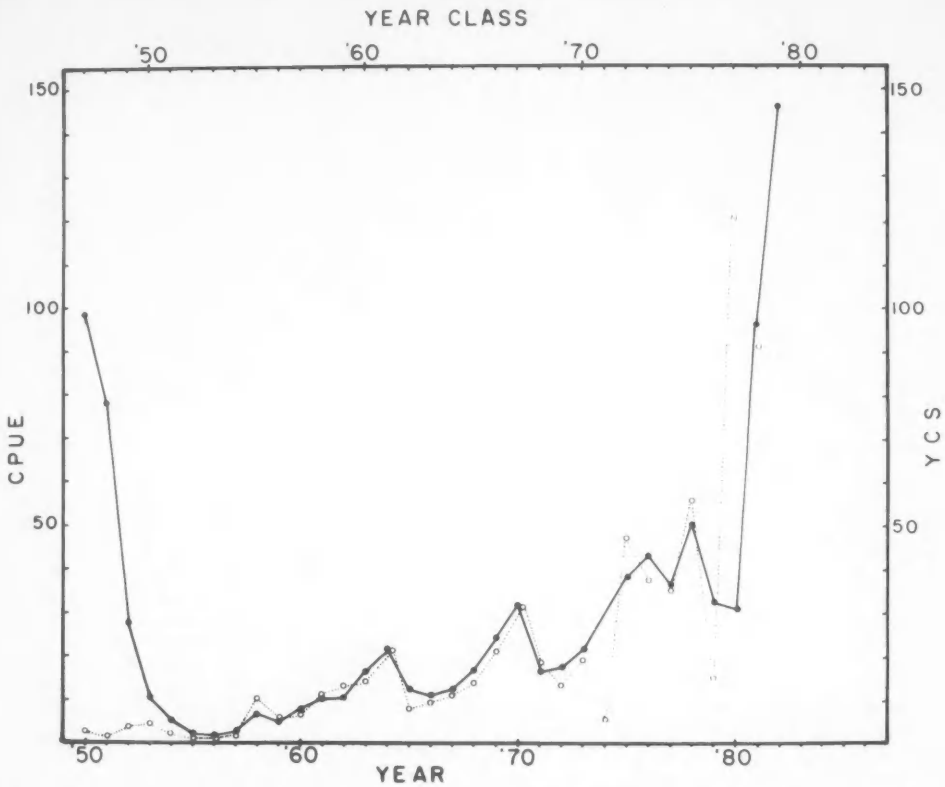

FIG. 4. Total CPUE of whitefish (>2 yr; 1950–82) solid circles, and relative year-class strength (YCS; 1947–78) open circles. Estimate of 1978 was based on only two age-classes (ages 3, 4).

early 1970s, commercial fishermen converted their gill nets from multifilament to monofilament web, a change which was shown experimentally to increase efficiency by 80% (Collins 1979). Contrary to our expectations, the correlation between the commercial and our experimental CPUE was lower when this correction for gear efficiency was applied ($r = 0.54$, $P < 0.05$). After the pound net catch was corrected for vulnerability to gill nets (114 mm), using Cucin and Regier's (1966) mesh selection coefficients, it was also less well correlated with the commercial catch ($r = 0.69$, $P < 0.05$).

Since 1960, catch, fishing effort, and exploitation rates have increased (Table 6). Exploitation rates (proportion of extant tags returned by commercial fishermen) were correlated with effort ($r = 0.86$, $P < 0.05$), excluding the years (1966–69) when too few vulnerable tags were available for capture (Table 6). Using these data describing population size, commercial catch (#s), and effort (km of 114-mm gill net), we were able to assess the hypothesis that catchability (q) declined as population size increased. Catchability was inversely related to population size ($r = -0.64$, $P < 0.01$, $y = 26.2169x^{-0.9649}$) (Fig. 7).

MORTALITY

Natural mortality (instantaneous rate = 0.779 ± 0.3040, $\bar{M}$ ± SD; finite rate = $\bar{n} = 0.54$; $\bar{n} = 1 - e^{-\bar{M}}$) was high and variable (range of $n = 0.34-0.81$) (Table 7). The natural mortality rate tended to increase for successive year-classes from 1950 to 1961, decreased to the lowest level for the 1971 year-class, then subsequently increased (Table 7). The fishing mortality rate was lower for the 1950 to 1962 year-classes (0.025 ± 0.0174, $\bar{F}$ ± SD, $\bar{m} = 0.02$) than for the later year-classes (1964–75) (0.221 ± 0.0426, $\bar{F}$ ± SD, $\bar{m} = 0.20$). The fishing rate varied with age — dependent upon the size selectivity of the commercial gill nets — and was highest for ages 4 and 5 (Table 8).

Discussion

Population size and year-class strength varied greatly during this study. From 1950 to 1956 the population size fell because of the attrition of the 1943 year-class and poor recruitment (Table 4, Fig. 4). Subsequently both population

TABLE 4. Annual catch-per-unit of effort of whitefish at each age, total CPUE > 2, and population estimate from 1950 to 1982 in pound net No. 6.

Year of catch	III	IV	V	VI	VII+	Nights set (effort)	CPUE > 2	Population size > 2	SE
1950	0.12	0.74	0.74	8.61	88.17	29	98.4	370 658	118 371
1951	0.63	1.88	0.63	0.75	74.44	29	78.3	301 409	92 209
1952	1.28	0.21	0.21	0.64	25.01	29	27.4	126 046	26 504
1953	0.21	1.51	0.34	0.21	8.29	29	10.6	68 166	7 999
1954	1.01	2.22	0.27	0.00	1.55	33	5.2	49 562	7 925
1955	1.00	0.37	0.58	0.04	0.24	33	2.2	39 226	10 249
1956	0.46	0.42	0.17	0.42	0.20	30	1.7	37 504	10 727
1957	0.66	0.61	0.24	0.38	1.09	26	2.9	41 638	9 615
1958	5.26	0.83	0.19	0.15	0.20	31	6.6	54 385	7 320
1959	2.49	2.05	0.18			31	4.7	47 839	8 229
1960	3.95	1.29	2.10	0.17	0.10	29	7.6	57 831	7 147
1961	6.20	1.87	1.32	0.94	0.03	31	10.4	67 477	7 885
1962	8.61	1.18	0.33	0.12	0.06	29	10.3	67 133	7 831
1963	11.00	3.21	1.68	0.36	0.37	28	16.6	88 838	13 481
1964	17.45	2.20	0.98	0.87	0.06	31	21.6	106 064	19 325
1965	6.30	3.85	0.79	0.43	0.68	31	12.1	73 334	9 052
1966	8.07	1.10	0.26	0.10	0.10	31	9.6	64 721	7 502
1967	8.92	1.62	0.45	0.14	0.03	31	11.2	70 233	8 381
1968	11.27	2.65	0.36	0.11		28	14.2	80 569	10 951
1969	16.18	4.00	0.48	0.22	0.08	27	21.3	105 030	18 962
1970	24.01	5.69	0.95	0.53	0.56	31	31.8	141 205	32 070
1971	11.41	4.26	0.89	0.07	0.07	27	16.7	89 182	13 591
1972	9.32	5.79	1.75	0.58	0.19	31	17.6	92 283	14 604
1973	16.18	3.72	1.15	0.48	0.41	27	21.9	107 098	19 689
1974	1.61	0.80	0.20	0.04	0.12	26	2.8	41 293	9 703
1975	20.49	2.30	1.69	0.29	0.36	28	38.5	164 288	40 638
1976	21.07	20.50	0.86	0.64	0.35	28	43.4	181 170	46 945
1977	20.03	11.35	4.45	0.32	0.35	31	36.6	157 743	38 201
1978	29.40	13.58	4.46	1.87	0.83	32	50.2	204 598	55 730
1979	8.86	21.17	1.21	0.55	0.82	28	32.6	143 962	33 088
1980	26.44	2.58	1.97	0.25	0.22	26	31.5	140 172	31 689
1981	34.45	54.73	2.66	2.23	1.32	28	96.4	363 768	115 767
1982	44.51	56.85	40.06	1.44	3.15	29	146.0	534 652	180 399

TABLE 5. Size at age [fork length, cm ± SD, (*N*)] for whitefish caught in pound net No. 6 during June 1950–82.

Years		2	3	4	5	6	7	8	9	10
1950–55	$\bar{x}$	29.6	38.6	42.4	44.0	46.1	43.9	44.0	45.3	48.1
	SD	2.03	2.08	2.60	3.45	2.62	3.13	2.41	2.73	3.40
	n	9	46	64	22	13	51	38	127	125
1956–60	$\bar{x}$	30.4	38.6	43.0	44.2	45.4	46.2	48.9	49.2	53.1
	SD	1.95	2.87	3.50	3.80	3.71	2.54	2.69	2.18	8.85
	n	355	320	136	99	27	21	7	4	3
1961–65	$\bar{x}$	29.4	37.6	42.8	42.6	42.1	43.7	46.0	0.0	0.0
	SD	1.67	2.39	3.66	4.62	3.54	3.91	0.98	0.0	0.0
	n	1182	1374	351	142	81	30	4	0	0
1966–70	$\bar{x}$	28.3	33.8	38.1	43.0	44.3	41.2	45.4	45.0	0.0
	SD	2.73	2.72	2.89	4.49	6.71	4.59	0.0	0.0	0.0
	n	1143	1936	757	165	37	25	1	1	0
1971–75	$\bar{x}$	26.8	31.6	42.6	46.9	48.9	47.2	44.5	53.6	44.3
	SD	2.06	2.56	2.84	4.36	4.72	8.68	6.87	6.51	0.25
	n	409	1762	555	171	49	22	12	2	3
1976–80	$\bar{x}$	25.6	32.8	39.2	44.9	48.9	50.4	53.1	55.2	48.8
	SD	2.24	2.33	2.62	3.20	3.53	5.88	5.91	4.30	3.47
	n	1052	3123	1994	423	109	32	23	8	8
1981–82	$\bar{x}$	26.3	33.1	39.9	45.2	48.3	49.9	52.6	55.6	57.8
	SD	1.90	1.95	2.27	2.55	3.52	4.75	6.01	8.20	0.0
	n	169	1186	1790	345	67	27	12	5	1

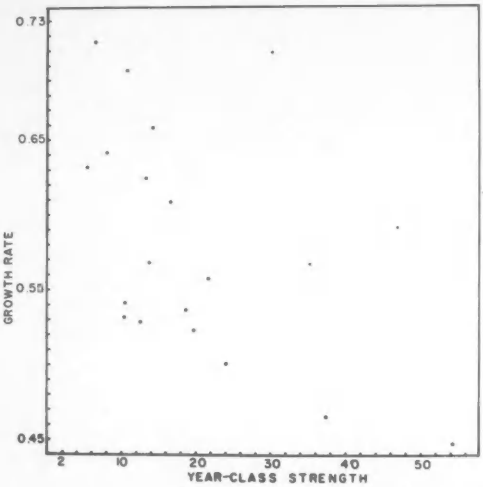

FIG. 5. Instantaneous growth rates (G) (mm fork length) from ages 2 to 3 in relation to relative year-class strength (CPUE units) from 1955 to 1977. The correlation was higher ($r = -0.78$, $P < 0.01$, $y = 0.927205x^{-0.180224}$) if the three fliers (◀) were excluded.

size and year-class strength increased. Two hypotheses about factors that regulated recruitment were assessed.

The first hypothesis assessed was that year-class strength

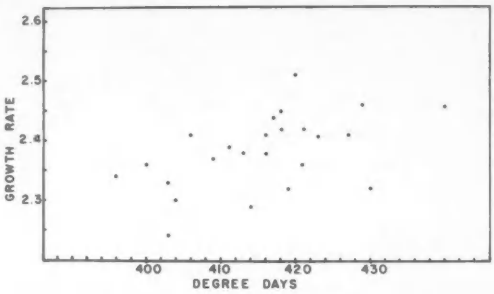

FIG. 6. Instantaneous growth rates (G) from ages 1 to 2 in relation to the degree days above 0°C from May to November in the years from 1955 to 1977.

was associated with the thermal regime during incubation. The statistical tests of this hypothesis were correlations between year-class strength and water temperature deviations in November and April, and Christie's (1963) thermal index. The hypothesis was rejected because none of these correlations was significant. Consequently, variations in the thermal conditions during spawning (November) and hatching (April) did not explain the observed variations in year-class strength.

The second hypothesis investigated was that year-class strength (recruitment) was a function of the size of the spawning stock size. The statistical test of this hypothesis was to determine if either a Ricker (1958) or Beverton and Holt

TABLE 6. Commercial catch and effort, catchability coefficients, and exploitation rate on tagged fish.[a]

Year	Catch (kg)	Catch (no.)	Effort (km)	CPUE (fish/km)	No. of vulnerable fish in population	q	Extant tags[b]	Proportion harvested[b]
1958	1 105	936	71.8	13.04	54385	0.000240	3382	0.03696
1959	1 181	1 001	47.6	21.03	47839	0.000440	3083	0.08725
1960	603	511	32.0	15.97	57831	0.000259	1884	0.0127
1961	182	154	19.2	8.02	67477	0.000119	2377	0.0551
1962	611	518	16.5	31.39	67133	0.000468	3216	0.0504
1963	1 212	1 027	43.0	23.88	88838	0.000269	3984	0.0959
1964	7 625	6 462	156.9	41.18	106064	0.000388	8794	0.0907
1966	7 943	6 731	234.1	28.75	64721	0.000444	1151	0.0139
1967	13 706	11 615	461.8	25.15	70233	0.000358	749	0.0027
1968	6 332	5 366	301.2	17.81	80569	0.000219	494	Nil
1969	10 885	9 224	381.9	24.15	105030	0.000230	269	0.0037
1970	12 476	10 573	457.8	23.09	141205	0.000164	632	0.0791
1971	4 785	4 055	158.0	25.66	89182	0.000288	867	0.0773
1972	20 813	17 638	610.0	28.91	92283	0.000313	980	0.3837
1973	8 442	7 408	248.1	29.85	107098	0.000279	1201	0.1690
1974	4 432	3 756	129.7	28.96	41293	0.000701	1049	0.1277
1975	14 773	12 519	210.0	59.61	164288	0.000363	1317	0.1590
1976	34 957	29 624	434.8	68.13	181170	0.000376	1468	0.2303
1977	22 965	19 461	429.9	45.27	157743	0.000287	1467	0.1970
1978	35 442	30 021	521.2	57.60	204598	0.000282	2682	0.2370
1979	55 464	46 946	819.3	57.30	143962	0.000398	1705	0.3736
1980	21 792	18 485	514.9	35.90	140172	0.000256	n.a.	n.a.
1981	15 755	13 336	322.9	41.30	363768	0.000113	n.a.	n.a.
1982	22 441	19 023	316.0	60.2	534652	0.000126	n.a.	n.a.

[a]No data available for 1965.
[b]n.a., not available.

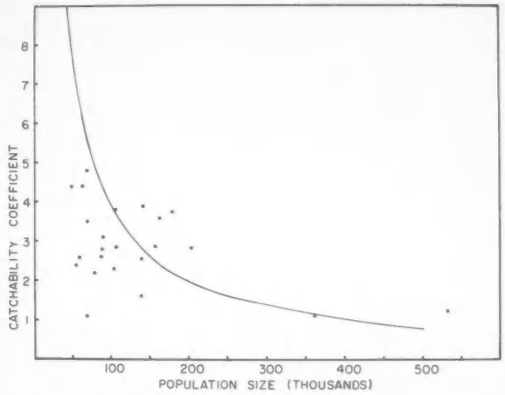

FIG. 7. The catchability coefficients (q) for whitefish caught in 144-mm-mesh gill nets at different population sizes.

(1957) recruitment curve explained a significant proportion of the variation in recruitment. The observed variation in recruitment was probably best described by a Ricker recruitment curve. However, 22 out of 25 data points were in one-sixth of the range of parental stock sizes (Table 1, Fig. 2). A linear regression of year-class strength on stock size through these points explained a significant part of the variation in recruitment for this range of data ($r = 0.53$, df = 22, $P < 0.05$). The poor recruitment during 1950–53, of progeny produced by the large 1943 year-class, constituted the only evidence of low recruitment at high parental stock sizes. With the available evidence one could not at least reject the hypothesis; recruitment was a function of stock size, but the precise nature of this relationship could not be ascertained unequivocally. Although there was little convincing data to confirm that recruitment either reached an asymptotic value (cf. Beverton and Holt 1957) or declined beyond an optimum stock size, there was some evidence for a density-dependent effect on recruitment. As stock size and egg production increased, there was a decline in the proportion of eggs that survived to 1-yr-old fish (Table 1, Fig. 3). This density-dependent mortality could be taken as further evidence that either a Ricker (1958) or Beverton and Holt (1957) type of recruitment curve could be applicable to this whitefish stock. Considering the spawning behavior of whitefish, we suggest that the Beverton and Holt (1957) curve would be more suited to whitefish, because there is little reason to believe that whitefish either compete for spawning substrate or destroy existing egg depositions through their spawning act, as other salmonids do (Ricker 1962). Density-dependent mortality could be the result of competition for food between young-of-the-year, resulting in the death of slowly growing fish. Alternatively adult whitefish may not spawn each year (Power 1978) if competition for food resulted in less energy being devoted to reproduction. In conclusion, recruitment was a function of parental stock size, early mortality was density dependent, but the exact form of the stock–recruitment relationship was unclear.

During the period when year-class strength and population size increased, the size of the fish at age 2 and 3 tended to decrease (Table 5). The decline in size could have been explained by increased competition for a limited food supply.

TABLE 7. Annual (A) and instantaneous (Z) total mortality, instantaneous (F) and conditional (m) fishing mortality, and instantaneous (M) and conditional (n) natural mortality rates for each year-class from 1947 to 1975 (ages 3–8).

Year-class	Z	A	F	m	M	n
1947	0.54	0.42				
1948	0.34	0.29				
1949	0.52	0.41				
1950	0.64	0.47	0.0068	0.01	0.6332	0.47
1951	0.45	0.36	0.0194	0.02	0.4306	0.35
1952	0.63	0.47	0.0057	0.01	0.6243	0.46
1953	0.44	0.36	0.0131	0.01	0.4269	0.35
1954	0.78	0.54	0.0141	0.01	0.7659	0.54
1955	0.83	0.57	0.0135	0.01	0.8165	0.56
1956	0.85	0.57	0.0154	0.02	0.8346	0.57
1957	1.14	0.68	0.0200	0.02	1.1200	0.67
1958	0.76	0.53	0.0220	0.02	0.7380	0.52
1959	1.09	0.66	0.0509	0.05	1.0391	0.65
1960	0.93	0.61	0.0553	0.05	0.8747	0.58
1961	1.72	0.82	0.0497	0.05	1.6703	0.81
1962	1.24	0.71	0.0379	0.04	1.2021	0.70
1963	0.69	0.50				
1964	0.96	0.62	0.2512	0.22	0.7088	0.51
1965	0.55	0.42				
1966	0.78	0.54	0.1907	0.17	0.5893	0.45
1967	0.78	0.54	0.1930	0.18	0.5870	0.44
1968	0.67	0.49	0.1504	0.14	0.5196	0.41
1969	0.75	0.53	0.1703	0.16	0.5797	0.44
1970	0.79	0.55	0.2093	0.19	0.5807	0.44
1971	0.55	0.42	0.2074	0.19	0.3426	0.29
1972	1.01	0.63	0.2481	0.22	0.7619	0.53
1973	1.19	0.70	0.2770	0.24	0.9130	0.60
1974	1.41	0.75	0.2603	0.23	1.1497	0.68
1975			0.2686	0.24		

TABLE 8. Instantaneous (F) and finite (m) fishing mortality rates on different age-classes for all year-classes combined.

	Age								
	2	3	4	5	6	7	8	9	10
F	0.01505	0.08192	0.15995	0.15639	0.10194	0.06976	0.06935	0.04252	0.02509
m %	1.5	7.9	14.8	14.5	9.7	6.7	6.7	4.2	2.5
	0.00247	0.0199	0.01686	0.00522	0.01091	0.00333	0.01005	0.00939	0.08961
Range	0.15415	0.40947	0.48811	0.59183	0.4397	0.28185	0.55431	0.3285	0.16705

The third hypothesis that growth was inversely related to abundance was tested statistically by first, correlating the instantaneous growth rates on year-class strength during the 1st, 2nd, and 3rd years of growth, and second, by correlating total CPUE in the pound net on size attained at age 2 and 3. Growth rate (G) was negatively correlated with year-class strength only for the 2nd year growth. Fork length at ages 2 and 3 were both inversely correlated with total abundance. Therefore, the hypothesis that growth was inversely related to abundance was not rejected.

First-year growth was correlated with the number of degree days above 0°C from May to November. Therefore, the fourth hypothesis, that growth was related to temperature was not rejected, at least for the 1st year of growth. Our measure of water temperatures was derived only from air temperatures (McCombie 1959) and was only applicable to surface waters frequented by young-of-the-year whitefish. Because young whitefish are less able physically to seek out optimum temperatures for growth, it may seem plausible that they would be more susceptible to changes in their thermal conditions. If reduced growth was the result of a limited supply of food, it could be envisaged that competition would have been most severe during the first season of growth when the year-class was most abundant. However, it was shown in a study of yellow perch (*Perca flavescens*) that also depended principally on plankton during part of their 1st year of growth, that the fish only consumed a small part of the total plankton biomass, and therefore food may not have limited growth and survival (Noble 1972).

Although the sizes at ages 2 and 3 declined with increasing population size, there was no evidence that the sizes of older fish also declined (Table 5). Any trend may have been obscured by the gill net fishery by only allowing fish at a certain size to escape. One of the implications of Healey's (1980) study was that growth was influenced by competition for food, so that an exploited population grew faster because there was more food per individual. From the available evidence that growth rates from ages 1 to 2 were inversely proportional to year-class strength, and that the size at age declined as population size increased, we concluded that Healey's (1980) hypothesis could not be rejected.

Our analysis of mortality rates showed that natural mortality rates were high and fishing rates were low (cf. Cucin and Regier 1966; Jensen 1976). The variation in natural mortality rates was probably largely explained by the abundance of sea lamprey (*Petromyzon marinus*) (Smith and Tibbles 1980). We did not monitor lamprey abundance or the frequency of lamprey wounds; however, lamprey-induced mortality was known to be high during the 1960s on the nearby Burnt Island whitefish stock (Spangler 1970; Spangler and Collins 1980).

During the late 1940s and early 1950s, there was an active commercial fishery on the abundant 1943 year-class. This large but slowly growing population was predominant in the catch from about 1947 until its demise by 1953. A commercial fishery on the South Bay stock (Casselman et al. 1981) did not start again until the early 1960s; the exploitation rate and effort increased with population size (Table 6). From 1960, 114-mm-mesh gill nets were used, but in recent years some 127-mm-mesh nets were employed to avoid large catches of white suckers (*Catostomus commersoni*). Apparently, the introduction of monofilament twine did not greatly improve catches. The modal age of the catch during this period was age 4. As a consequence, whitefish were harvested at about the age of maturation, and the success of the fishery was dependent upon variations in year-class strength.

The proportion of the population harvested per unit of effort declined as population abundance increased (Fig. 7). Thus, the fifth hypothesis, that catchability (q) was inversely related to abundance, was not rejected. However, the statistical significance of the result depended entirely on two extreme years (1981 and 1982), without which the result was insignificant. There are at least two possible explanations, apart from chance, for this inverse relationship between catchability and abundance. First, as the population size and catch increases, the gear becomes progressively saturated, and thus its efficiency declines; fish entangled in nets may deter other fish. There are two disturbing implications of this inverse relationship between catchability and abundance. First, gill net CPUE may be an unreliable index of abundance because the 'efficiency' of the gear changes with abundance. However, over a large range of abundances, there was only a small change in (q) (Fig. 7), so that in most situations CPUE in gill nets would probably be correlated with the abundance of vulnerable fish. Second, fishing effort may exact a greater toll than at lower densities; theoretically at least, this would increase the probability of the extirpation of small populations. However, the CPUE would probably be too low to attract a fishery. The second explanation of this inverse correlation between q and N is that as the population abundance and harvest declines, the fishery becomes more selective in the placement of nets (to maintain CPUE), and thus only sets at times of the year when catches are best (inshore during the spring and on the spawning shoal in the autumn) or at favored locations.

Apart from the evidence provided by studies of whitefish by Healey (1975, 1980), there has been little evidence for an intrinsic mechanism of population regulation (Christie 1963; Jensen 1981). We propose a model in which potential recruitment is a function of parental stock size, but it is adjusted by a density-dependent rate of survival from the egg to juvenile stage. This relationship may be a direct function of mortality on eggs or young. Alternatively, a similar result would occur if proportionately fewer females spawned annually as the population increased. Density-dependent regulation of recruitment is enhanced by density-dependent growth, resulting in variations in the age of spawning. Faster growing year-classes mature earlier and produce more offspring than later maturing year-classes that have experienced more years of natural mortality before spawning. The commercial fishery can act as a density-dependent factor by removing proportionately more fish as the population size increases.

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Relative Importance of Substrate Particle Size and Detritus to Stream Benthic Macroinvertebrate Microdistribution

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CULP, J. M., S. J. WALDE, AND R. W. DAVIES. 1983. Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. Can. J. Fish. Aquat. Sci. 40: 1568–1574.

Manipulative field experiments were conducted in Carnation Creek, British Columbia, to determine whether particle-size composition of the stony substrate influenced macroinvertebrate microdistribution if substrate detritus was standardized. A standardized quantity of alder (*Alnus rubra*) detritus was added to five substrate mixtures ranging from homogeneous gravel to a heterogeneous gravel, pebble, and cobble mixture, and the substrates imbedded in a riffle to allow macroinvertebrate colonization. Densities and biomasses of most macroinvertebrate taxa (16 of 19) were not significantly different among the wide range of substrate types containing the standardized alder detritus, even though surface area, intrasubstrate current velocity, and interstitial space varied significantly between treatments. However, in the treatment that did not have the standardized detritus, the biomasses and densities of nine taxa, and the totals of all taxa combined, were significantly lower than in an identical substrate mixture that contained the detritus. We concluded that the differential colonization of substrates demonstrated for many macroinvertebrate taxa in previous studies was more likely related to differences in organic sedimentation. Although detritus is a major determinant of detritivore microdistribution, substrate composition may be an important factor to other trophic groups such as filter-feeders.

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Des expériences de manipulation sur le terrain ont été menées dans le ruisseau Carnation, en Colombie-Britannique, en vue de déterminer si la grosseur des particules influence la microdistribution des macro-invertébrés quand les détritus du substrat sont standardisés. Une quantité standardisée d'aulne (*Alnus rubra*) a été ajoutée à cinq mélanges de substrats, variant d'un gravier homogène à un gravier hétérogène, un mélange de cailloux et de moellons, et des substrats enrobés dans un « maigre », afin de permettre la colonisation par les macro-invertébrés. Les densités et biomasses de la plupart des taxa de macro-invertébrés (16 sur 19) ne diffèrent pas de façon significative dans une gamme étendue de types de substrats contenant des détritus d'aulne standardisés, même si l'étendue de la surface, la vitesse du courant dans le substrat et l'espace interstitiel varient notablement d'un traitement à l'autre. Cependant, dans le traitement sans détritus standardisés, des biomasses et densités et 9 taxa, ainsi que les totaux de tous les taxa combinés sont nettement plus faibles qu'avec un mélange de substrats identiques contenant les détritus. Nous concluons que les différences démontrées dans la colonisation de substrats par plusieurs taxa de macro-invertébrés au cours d'études antérieures étaient probablement liées à des différences de sédimentation organique. Bien que les détritus soient un facteur majeur dans la microdistribution des détritivores, la composition du substrat peut être importante pour les autres groupes trophiques, tels que les filtreurs.

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MACROINVERTEBRATE distribution and abundance has been correlated with several interrelated variables including substrate composition (Linduska 1942; de March 1976), current velocity (Minshall and Minshall 1977), and the quantity of organic detritus in the substrate (Egglishaw 1964). Researchers have often attempted to determine the importance of substrate by examining the short-term (<30 d) colonization of different substrate treatments while controlling current

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velocity (Allan 1975; Minshall and Minshall 1977; Williams and Mundie 1978; Khalaf and Tachet 1980; Reice 1980; Williams 1980). Although in a few of these studies total detritus accumulation was measured at the end of the experiments, no attempt was made to control detritus particle size or quantity. Because the particle sizes and quantities of detritus trapped within the streambed may be greatly influenced by substrate composition (Rabeni and Minshall 1977), and because macroinvertebrates often use detritus of a specific particle size for food (Cummins 1973), the effect of detritus accumulation on the results of these substrate composition experiments cannot be determined.

Unlike previous experimental manipulations of substrate composition where detritus was not standardized, in our study substrate particle size and heterogeneity were the only experimental variables. Thus, the objective of this study was to determine if stony substrate ranging from gravel to cobbles influenced the distribution and abundance of benthic macroinvertebrates.

Study Area

Carnation Creek is a third-order (sensu Strahler 1957) stream in the Coastal Western Hemlock biogeoclimatic zone (Klinka et al. 1979), which flows directly into Barkley Sound on the west coast of Vancouver Island, British Columbia. The stream drains a 10-km^2 area, 41% of which has been clear-cut. Annual rainfall is high (280–350 cm/yr), and stream discharge can vary from a summer minimum of 0.015 m^3/s to 4.25 m^3/s during winter storms (Stockner and Shortreed 1976). Experiments were conducted in a logged stream reach where the riparian tree and shrub vegetation consisted primarily of red alder (*Alnus rubra*), with salmonberry (*Rubus spectabilis*), salal (*Gaultheria shallon*), and occasional large western hemlock (*Tsuga heterophylla*) or Sitka spruce (*Picea sichensis*).

Materials and Methods for Substrate Experiments

Substrate was obtained from dry areas of the streambed and sieved into size classes corresponding to the modified Wentworth scale (Cummins 1962). Five substrate mixtures were produced: G, homogeneous large gravel (9.5–16.0 mm); P, homogeneous small pebbles (16.0–31.5 mm); GP, a 1:1 volumetric mixture of gravel and pebbles; GPS, a 1:1 gravel and pebble mixture with the interstices filled with small–medium gravel and coarse sand (1.0–9.5 mm); GPSC, an identical mixture to treatment GPS with cobble (50.0–80.0 mm) on the surface, that approached the habitat complexity of the natural substrate.

Detritus of standardized source and quantity was added to each of these five substrate types; a sixth treatment (GP–ND) with the same substrate composition as treatment GP contained no detritus. The surface layer of substrate in each treatment consisted of rocks collected from an upstream riffle so that the treatments were standardized with a visually similar periphyton growth. The range in substrate composition between treatments G to GPSC was chosen because it encompasses most composition used in previous substrate experiments (e.g. Minshall and Minshall 1977; Rabeni and Minshall 1977; Williams and Mundie 1978; Khalaf and Tachet 1980; Reice 1980; Williams 1980). Similarly, the quantity of detritus corresponds to the amount used in previous detritus manipulative experiments (e.g. Rabeni and Minshall 1977; Peckarsky 1980).

The degree of microbial conditioning and quantity of the detritus added to substrate treatments G, P, GP, GPS, and GPSC were standardized so that substrate composition was the only experimental variable among the treatments. Detritus was produced by collecting alder leaves from trees that had been felled 5 wk earlier. The alder leaves were then incubated for 4 wk in flowing creek water from which invertebrates had been removed by filtering, and in the dark to prevent algal photosynthesis. Immediately, prior to experiment initiation, the microbially conditioned leaves were mechanically shredded in a blender and wet-sieved into fine (230–850 μm) and medium (850–2000 μm) fractions.

Four cylindrical plastic containers (0.015 m^2, 6.5 cm deep) per treatment, with two 230-μm-mesh windows (21.0 × 3.5 cm) to allow water flow through the container, were filled with the appropriate substrate and 7.5 g wet mass (100 g/m^2 dry mass) of alder detritus (fine to medium ratio 2:1). The containers were momentarily sealed and implanted into the experimental riffle so the upper edges were flush with the streambed surface. The covers were immediately removed, and the containers left in the stream for a 31-d colonization period (July 21–August 20, 1980). Timing of the experiment corresponded with the hot dry period when leaf abscission is high, and leaf packs are common in the riffle substrate. The containers were open at the top, and all size classes of macroinvertebrates that were swimming, drifting, or crawling in the upper 3 cm of streambed could freely access the containers. Smaller invertebrates could also enter via the 250-μm-mesh side screens. Because >50% of the benthos in the upper 10 cm of streambed occurs at the surface (upper 3 cm), and because most taxa are commonly found in the drift (Culp 1982), the container design provided adequate accessibility to invertebrates.

The containers were carefully removed at the end of the experiment, community respiration was measured on the undisturbed sediments using methods modified from Osborne and Davies (1980), and the macroinvertebrates and detritus from each container were preserved in 10% formalin. Subsequently, macroinvertebrates were sorted under 12× magnification, identified to the lowest taxonomic level possible, enumerated, and the dry biomass of each taxon measured using a Cahn 25 automatic electrobalance. The ash-free dry mass of the detritus was also determined.

Sedimentation could potentially affect the substrate composition of the experimental containers, thus, the amount of fine inorganic and organic sediments accumulated by each substrate type was examined. At the beginning of the experimental period, four replicate sediment traps (0.005 m^2) (Welton and Ladle 1979) for each substrate treatment were placed into the experimental riffle. At the end of the experiment the traps were emptied, their contents dried at 60°C for 48 h and ashed at 500°C for 24 h, and the dry mass of the organic (i.e. ash-free dry mass) and inorganic sediments determined.

Abiotic losses of alder detritus from the containers could also change the experimental treatments. This potential loss was measured in treatment F by soaking substrate mixtures identical with those of treatment GP in concentrated formalin, and placing them immediately downstream of the experimental riffle. These containers were removed every 5–7 d during the experiment, immersed in formalin for 4 h, and replaced in the stream. At the end of the experiment the contents of the containers of the formalin treatment were preserved, the detritus dried at 60°C for 48 h, and the dry mass determined.

Physical variables were also measured during the course of the experiment. Current velocity 2.5 cm above the substrate was measured at the start and end of the experiment for each substrate treatment with a Gurley pygmy current meter. Additionally, a salt dissolution technique (Rabeni and Minshall 1977) was used to measure intrasubstrate current velocity in containers placed immediately downstream of the experimental area. Discharge was continuously monitored throughout the experiment by Environment Canada.

The total volume of interstitial space in substrate treatments G, P, and GP was measured in the laboratory by adding water to containers with the substrate mixtures, and recording the decanted water volume. Surface area of particles in treatments G, P, GP, GPS, and GPSC were determined by inking the surface of a known volume of rocks with a 0.5-cm^2 stamp for gravel, and a 1-cm^2 stamp for pebble and cobble. Surface area estimates for treatments GPS and GPSC are conservative as sand-particle surface area was not determined.

Statistical Methods

We used Model I ANOVA (Zar 1974) to determine whether the substrate compositions of treatments G, P, GP, and GPSC significantly affected macroinvertebrate density and biomass transformed to $\log(x + 1)$ (Elliott 1977), the retention of fine and medium detritus in the substrate, community respiration, organic and inorganic sedimentation, current velocity within and above the substrate, interstitial space, and substrate surface area. If differences among the treatments were significant, the Student–Newman–Keuls (SNK) multiple-range test (Zar 1974) was used to establish the significantly different treatment(s).

The effect of detritus on macroinvertebrate colonization was determined by using Student's *t*-test (Zar 1974) to compare mean values of macroinvertebrate density and biomass in the treatment with detritus (GP) to values in a similar substrate without detritus (GP–ND). Furthermore, multiple correlation coefficients (Zar 1974) for macroinvertebrate density or biomass with fine and medium detritus were calculated to establish whether macroinvertebrate colonization in treatments G to GPSC was correlated with the amount of detritus retained in the substrate at the end of the experiment. When multiple correlation coefficients were significant, the partial correlation coefficient of each independent variable (i.e. fine or medium detritus) was determined (Zar 1974). Note that for all analyses the data were normally distributed and homoscedastic, and hypothesis rejection was performed at the $P = 0.05$ level of probability.

Results

Abiotic Environmental Conditions

During the experimental period water temperature ranged from 12.0 to 14.0°C, pH from 6.8 to 7.2, and total alkalinity from 16.5 to 20.3 mg/L $CaCO_3$. Current velocity also was similar throughout the experiment (15–31 cm/s) and no significant differences between the treatments were recorded. Mean daily discharge ranged from 0.042 to 0.062 m^3/s for most of the experimental period; however, during the 1st wk discharge reached a peak of 0.116 m^3/s. Only small amounts of organic sediments (i.e. detritus) were suspended and redeposited by these discharge levels, as at the end of the experiment, accumulations of detritus in the sediment traps accounted for <60 mg of the detritus in each treatment container. Furthermore, the amount of detritus deposited was similar for all treatments. Inorganic sedimentation, as measured by sediment traps, was <200 mg per container regardless of the substrate treatment.

Results of Substrate Manipulations

Intrasubstrate current velocity, substrate surface area, and total interstitial space varied significantly between substrate treatments (Table 1). Total volume of interstitial space was highest in pebble substrate (P) and lowest in gravel substrate (G), and among the gravel, pebble, and gravel–pebble treatments interstitial space was inversely related to surface area. (Although not measured, total interstitial space must have been even lower in treatments GPS and GPSC where sand occupied the interstitial pores.) Conversely, intrasubstrate current was positively related to total interstitial space, except in treatment P, where intrasubstrate current was unexpectedly low presumably because relatively large plumes of calm water were formed in the interstices downstream of each pebble.

About 50–60% of the amount of fine and 30–40% of the medium detritus placed in the containers was present at the end of the experiment in substrate treatments G, P, GP, GPS, and GPSC, except for the pebble treatment (P) where losses were significantly higher (Fig. 1). As the final amount of detritus in the abiotic formalin treatment was similar to the amounts recorded for treatments G, P, GP, GPS, and GPSC, the losses of detritus during the experiment were largely the result of abiotic processes (Fig. 1). Although the total amount of detritus was reduced in the treatments, the losses attributable to abiotic processes did not affect the initial 2:1 fine-to-medium ratio of particle sizes as was demonstrated for the formalin treatment (F) (Fig. 1). However, in the treatments colonized by macroinvertebrates, the final ratios of particle sizes increased from the original 2:1 ratio to 2.7–4:1 (Fig. 1). Comparing all substrate treatments with macroinvertebrate colonization (G, P, GP, GPS, and GPSC), the decreases in medium-sized and fine detritus particles were significantly higher in the pebble treatment, which by inspection was determined to have the largest average volume per individual interstitial pore space.

The substrate treatments had no effect on the amount of community respiration standardized per unit mass of detritus, but absolute community respiration varied significantly

TABLE 1. Comparison of the mean value of absolute community respiration, standardized community respiration, intrasubstrate current, surface area, and interstitial space recorded for the six treatments. (Community respiration data were not available for treatments G or GP−ND as a result of equipment failure.)

	Substrate treatment					
	G	P	GP	GPS	GPSC	GP−ND
Absolute community respiration (CO_2 mg/L)	—	0.50	0.79	0.96	0.84	—
Standardized community respiration (CO_2 mg·L^{-1}·mg^{-1} detritus)	—	1.07	1.23	1.16	1.16	—
Intrasubstrate current (cm/s)	6.4	3.5	9.3	4.2	3.3	9.3
Surface area (m^2)	0.31	0.11	0.21	>0.21	>0.19	0.21
Interstitial space (cm^2)	420	474	435	<435	<435	435

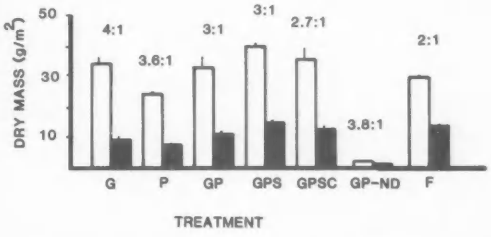

FIG. 1. Mean dry mass of the remaining fine (white) and medium (black) detritus, and the fine-to-medium ratio of gravel (G), pebble (P), gravel−pebble (GP), gravel−pebble−sand (GPS), and the gravel−pebble−sand−cobble (GPSC) substrate treatments, and the abiotic formalin treatment (F).

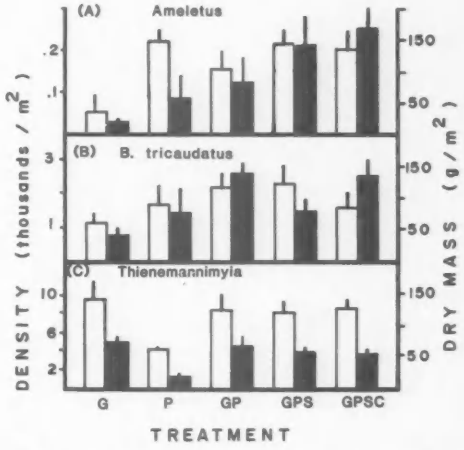

FIG. 2. Mean density (white) and biomass (black) of *Ameletus*, *B. tricaudatus*, and *Thienemannimyia* in the gravel (G), pebble (P), gravel−pebble (GP), gravel−pebble−sand (GPS), and gravel−pebble−sand−cobble (GPSC) substrate treatments.

between substrate types (Table 1). Treatment GPS, which retained the greatest amount of fine detritus, had a significantly higher absolute community respiration rate than P (Table 1) which retained the least fine detritus. Absolute community respiration was positively correlated with both detritus dry mass and macroinvertebrate biomass ($r^2 = 0.77$), but subsequent partial correlation analyses indicated the significant relationship was between community respiration and fine detritus dry mass ($r^2 = 0.51$).

A Model I ANOVA demonstrated that the mean densities and biomasses of only 3 of 19 macroinvertebrate taxa that colonized the containers showed significant differences between the substrate treatments with the standardized detritus added (G, P, GP, GPS, and GPSC) (Fig. 2). The trends of low density and biomass of *Thienemannimyia* in the pebble treatment were associated with significantly lower levels of detritus. SNK tests further established that the biomasses of the collectors *Baetis tricaudatus* and *Ameletus* were significantly lower in the homogeneous gravel (G) substrate compared to treatments P, GP, GPS, and GPSC.

It was surprising that the distributions of most taxa colonizing treatments G, P, GP, GPS, and GPSC were not affected by the large differences in substrate particle size when detritus quantity and quality were standardized. However, the gravel−pebble treatment without detritus (GP−ND) had a significantly lower biomass for nine taxa and lower density for eight taxa compared to the gravel−pebble treatment with the standardized detritus mixture (Table 2). These nine taxa comprised over 60% of the total macroinvertebrate density and biomass of the gravel−pebble with detritus, and except for two predators (*Skwala* and *Thienemannimyia*), were shredders or collectors. Furthermore, the detritivores *Brillia* and *Parametriocnemus*, which were present in the gravel−pebble (Table 2) and all other substrate treatments with detritus, were absent in the no-detritus treatment (Table 2).

Although the amount of detritus in treatments G, P, GP, GPS, and GPSC was initially standardized, small differences in detritus retention among the treatments were noted, and the mean densities and/or biomasses of four taxa were significantly correlated with the dry mass of fine and medium detritus that remained in substrates G, P, GP, GPS, and GPSC at the end of the experiment (Table 3). Biomasses of the shredders *Zapada cinctipes* and *Polypedilum* (*Polypedilum*) which comminute medium particles, and the collector

TABLE 2. Biomass (g/m^2) and density (thousands/m^2) for the nine macroinvertebrate taxa which exhibited statistically significant differences between the gravel and pebble substrate with (GP) and without detritus (GP−ND), and the significantly different totals for all 19 taxa that colonized the experimental containers. (15 taxa with mean treatment values of less than one individual per replicate were omitted from the analysis.)

Taxon	Biomass		Density	
	GP	GP−ND	GP	GP−ND
Baetis tricaudatus	0.13	0.04	2.18	0.86
Brillia	0.56	0	3.70	0
Chironomidae pupae	0.40	0.01	1.85	0.07
Micropsectra	0.04	0.01	3.10	1.12
Parametriocnemus	<0.01	0	0.20	0
Polypedilum (*Polypedilum*)	0.69	0.01	8.05	0.66
Skwala	0.13	0.01	1.85	0.06
Thienemannimyia	0.07	0.01	8.58	2.05
Zapada cinctipes	0.01	<0.01	0.07	0.07
Total for all 19 taxa	3.17	1.58	43.30	17.09

Micropsectra, were negatively correlated with medium detritus mass, and positively correlated with fine detritus mass. Densities of *Z. cinctipes* and *Thienemannimyia* were positively correlated with fine detritus mass, but only *Z. cinctipes* showed a negative correlation with medium detritus mass.

Discussion

Constancy of Experimental Conditions

For field manipulative experiments to be valid, it must be demonstrated that environmental conditions during the experiment did not significantly alter the treatment variables, and that treatment replicates were constant. The Carnation Creek substrate experiment meets this requirement because the minute amounts of detritus and inorganic sediments collected in the sediment traps of each substrate type during the colonization period did not significantly alter any of the treatments, and because all the replicates within each treatment were similar. Although the formalin treatment (F) indicates that abiotic processes decreased the fixed amounts of detritus initially added to the containers, this abiotic loss did not greatly affect the experimental design because final detritus quantities were similar for all treatments, except treatment P which had less detritus. The higher loss of detritus from the pebble treatment probably occurred because the large interstitial pore spaces between the pebbles did not trap the added detritus as effectively as did the smaller interstitial pore spaces of the four other substrate treatments.

Effect of Substrate Manipulation on Macroinvertebrate Colonization

The design of the substrate experiment allowed the influence of substrate particle size upon macroinvertebrate colonization to be delimited because the source and microbial conditioning (sensu Boling et al. 1975) of the detritus in the substrates was carefully standardized, and sedimentation did not change experimental conditions. Despite the wide range of particle size and substrate heterogeneity which the substrate types spanned, only *Thienemannimyia*, *B. tricaudatus*, and *Ameletus* exhibited significant differences between the treatments (Fig 2). The significant differential colonization of substrates by the predator *Thienemannimyia* was associated with the slightly lower detritus retention and prey densities in the pebble treatment, but the colonization of *B. tricaudatus* and *Ameletus* did not correspond to any trend of the measured variables (i.e. measured changes in detritus, interstitial space, intrasubstrate current, surface area), and are an enigma. Reice (1980) has suggested that macroinvertebrate densities expressed as a function of rock surface area can provide more meaningful ecological information than the more standard expression of density per unit area (m^2) of streambed surface. However, the Carnation Creek study obtained results similar to Rabeni and Minshall (1977), where the lack of a trend between macroinvertebrate distribution and substrate surface area was found. This demonstrates that the expression of macroinvertebrate density per unit of rock surface area often may not be warranted, and certainly, that a correlation between macroinvertebrate density and rock surface area cannot be assumed

Although our study indicates that macroinvertebrate distribution was not affected by the total amounts of interstitial space in the substrate treatments, this pooled measurement of the substrate interstices does not attempt to delineate the volume, number, or geometric shape of individual interstitial pores. Each of these may be biologically relevant components of interstitial space that vary with substrate composition and,

TABLE 3. Comparison of the multiple r^2 values and the partial correlation coefficients for the four macroinvertebrate taxa in the gravel, pebble, gravel−pebble, gravel−pebble−sand, and gravel−pebble−sand−cobble substrate treatments which showed significant multiple correlation coefficients between final density (no./m^2) or biomass (g/m^2) and the final amount of fine and medium detritus. (— indicates not significant.)

Taxon	Multiple r^2		Correlation with fine detritus		Correlation with medium detritus	
	no./m^2	g/m^2	no./m^2	g/m^2	no./m^2	g/m^2
Micropsectra	—	0.31	—	+0.55	—	−0.40
Polypedilum (*Polypedilum*)	—	0.33	—	—	—	−0.50
Thienemannimyia	0.27	—	+0.40	—	—	—
Zapada cinctipes	0.26	0.38	+0.39	+0.50	−0.51	−0.62

thus, need to be more fully investigated in future studies.

Statistically significant reductions in the biomasses and densities of nine taxa, and the totals for all macroinvertebrates, resulted when treatment GP−ND (alder detritus absent) was compared with treatment GP which had identical pebble and gravel substrate (alder detritus added). Thus, these experimental results indicate that detritus was a more important microdistribution factor than substrate composition. Although the amount of detritus remaining at the end of the experiment was relatively constant between treatments G, P, GP, GPS, and GPSC, correlation analyses showed that a few detritivores (*Z. cinctipes, Polypedilum, Micropsectra*) were influenced by even the small differences in the final amounts of fine and medium detritus in these substrates (Table 3), but not by substrate composition. The importance of alder detritus as a microdistribution factor may be because of its use by detritivores as a food resource. That detritus was used as a food source is suggested by the biotic processing which increased the fine-to-medium detritus particle ratio probably as a result of detritivore comminution. Furthermore, partial correlation analysis indicated that community respiration in the containers was largely attributable to microbes associated with the detritus.

Equivocal results were obtained in earlier substrate experiments (Rabeni and Minshall 1977; Williams and Mundie 1978; Wise and Molles 1979; Khalaf and Tachet 1980; Reice 1980) because the influence of detritus and substrate composition could not be separated. These studies found that the highest macroinvertebrate density or biomass occurred in the gravel-to-pebble substrate size range (10−40 mm), or in slightly larger substrates (16−64 mm; Allan 1975). Indeed, Rabeni and Minshall (1977) hypothesized that high detritivore abundance in gravel and pebble reflects the greater accumulation of detritus by these substrates, rather than the direct effect of substrate particle size. However, they could not clearly demonstrate this because their treatment variables were greatly altered by environmental conditions. The Carnation Creek experiment demonstrated that, when the source and quantity of the detritus in the streambed was standardized, the density and biomass of detritivores was not affected by wide differences in substrate composition ranging from large gravel to small pebbles.

Macroinvertebrate microdistribution is hypothesized to be the result of species-specific responses to important environmental gradients such as current velocity, substrate particle size, and food resources (Cummins and Lauff 1969; Rabeni and Minshall 1977), and also biotic interactions (Peckarsky and Dodson 1980a, 1980b). Our interactive experimental design eliminated current velocity as an experimental variable, and demonstrated that the microdistribution of many detritivorous taxa centered upon the presence or absence of detritus food particles, rather than particular substrate types. As has been noted in Carnation Creek (Culp 1982), detritus is also expected to have an accentuated importance as a microdistribution factor in other streams where shredder and collector detritivores are the dominant trophic guilds. This is not to say, however, that substrate composition could not be an important determinant of microdistribution for other trophic groups, as for the filter-feeders which need appropriate attachment sites (Khalaf and Tachet 1980).

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Effects of Low pH on Eyed Embryos and Alevins of Pacific Salmon

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ROMBOUGH, P. J. 1982. Effects of low pH on eyed embryos and alevins of Pacific salmon. Can. J. Fish. Aquat. Sci. 40: 1575–1582.

Ten-day bioassays were conducted to assess the sensitivity of eyed embryos, newly hatched alevins, and buttoned-up alevins of coho (*Oncorhynchus kisutch*), chinook (*O. tshawytscha*), sockeye (*O. nerka*), pink (*O. gorbuscha*), and chum (*O. keta*) salmon to low pH. Acid sensitivity varied significantly both with stage of development and with species. The various stages and species were ranked in order of decreasing sensitivity to low pH on the basis of significant differences ($P < 0.05$) in 10-d LC50 values. Stage sensitivities (10-d LC50 pH range) were ranked buttoned-up alevins (4.4–5.2) > newly hatched alevins (4.4–4.9) > eyed embryos (3.6–4.0) for all species except coho. Coho were more sensitive as newly hatched alevins than near button-up. Species sensitivities were ranked (chum, pink) > sockeye > chinook > coho for eyed embryos, coho > (chinook, sockeye) > (pink, chum) for newly hatched alevins, and (chum, pink, sockeye) > chinook > coho for buttoned-up alevins. Ten-day LC10s for eyed embryos ranged from pH 3.82 for chinook to pH 4.18 for chum. LC10s for the most sensitive alevin stage of each species ranged from pH 5.01 for coho to pH 5.74 for chum. Incipient lethal levels could not be estimated for any stage or species because no toxicity curves approached a pH threshold during the test period. Aberrant behavior was noted in buttoned-up alevins of pink and chum exposed to pH 6.0–6.1 but not in other species at levels above those causing acute mortality.

ROMBOUGH, P. J. 1982. Effects of low pH on eyed embryos and alevins of Pacific salmon. Can. J. Fish. Aquat. Sci. 40: 1575–1582.

Des essais biologiques de 10 jours ont été menés en vue d'évaluer la sensibilité à un bas pH d'embryons oculés, d'alevins nouvellement éclos et d'alevins après résorption du vitellus des espèces de saumons suivants : coho (*Oncorhynchus kisutch*), chinook (*O. tshawytscha*), nerka (*O. nerka*), rose (*O. gorbuscha*) et keta (*O. keta*). La sensibilité à l'acide varie de façon significative en fonction du stade de développement de l'espèce. Les divers stades et espèces ont été rangés par ordre de sensibilité décroissante à un bas pH selon les différences significatives ($P < 0{,}05$) de valeurs de CL50 après 10 jours. L'ordre de sensibilité des divers stades (la gamme de pH de CL50 après 10 jours est indiquée entre parenthèses) est le suivant : alevins sans vitellus (4,4–5,2) > alevins nouvellement éclos (4,4–4,9) > embryons oculés (3,6–4,0), pour toutes les espèces, sauf le saumon coho. Ce dernier est plus sensible au stade l'alevin nouvellement éclos qu'après résorption du vitellus. L'ordre de sensibilité des espèces est le suivant : (keta, rose) > nerka > chinook > coho pour les embryons oculés, coho > (chinook, keta) > (rose, keta) pour les alevins nouvellement éclos et (keta, rose, nerka) > chinook > coho pour les alevins sans vitellus. La CL10 après 10 jours pour les embryons oculés varie d'un pH de 3,82 dans le cas du saumon chinook à 4,18 dans celui du saumon keta. Les CL10 du stade d'alevin le plus sensible de chaque espèce varient d'un pH de 5,01 chez le saumon coho à un pH de 5,74 chez le saumon keta. Il a été impossible d'estimer les niveaux de début des mortalités d'aucun stade ou espèce car, durant toute la période de l'expérience, aucune courbe de toxicité n'approcha un seuil de pH. Un comportement anormal a été observé chez des alevins de saumons rose et keta après résorption du vitellus, exposés à des pH de 6,0–6,1, mais non chez les autres espèces, à des niveaux supérieurs à ceux produisant des mortalités aiguës.

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THE problem of surface water acidification and the resulting decline in fish populations has been examined extensively in eastern North America (Beamish et al. 1975; Farmer et al. 1980) and Scandinavia (Jensen and Snekvik 1972; SNSF 1980). Affected fish populations usually decline because of recruitment failure (Beamish et al. 1975). Laboratory studies indicate that the period between fertilization and yolk absorption is one of high sensitivity to low pH (Menendez 1976; Daye and Garside 1977, 1979; Johansson et al. 1977; Peterson and Martin-Robichaud 1982), and observations in the field suggest that mortality during this period is the most common reason for the loss of salmonid populations from acid

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waters (Jensen and Snekvik 1972; Rosseland et al. 1980).

In recent years there appears to have been a trend toward more acidic precipitation in regions of western North America (Anon. 1981; Rubec 1981). The Pacific salmon (genus *Oncorhynchus*) native to the area are of major economic importance and the implications of a decline in their abundance due to surface water acidification would be substantial. Yet, there is no information available on the influence of acid pH levels on early developmental stages of these species. My objective was to evaluate the sensitivity of eyed embryos, newly hatched alevins, and buttoned-up alevins of five species of Pacific salmon to low pH.

Materials and Methods

A series of 10-d bioassays was conducted to determine the acute toxicity of acidified water to eyed embryos [Vernier (1969) stages 28–29], newly hatched alevins (stages 30–31), and buttoned-up alevins (stage 37) of coho (*Oncorhynchus kisutch*), chum (*O. keta*), pink (*O. gorbuscha*), sockeye (*O. nerka*), and chinook (*O. tshawytscha*) salmon.

Gametes of the various species to be tested were obtained from fish returning to spawn in the Fulton River in northwestern B.C. (sockeye), the Quinsam River, Vancouver Island (pink), and the Big Qualicum River, Vancouver Island (chinook, chum, and coho). Gametes from 4 to 10 individuals of the same sex were pooled. The eggs and milt were stored separately at 1–5°C and transported to the Pacific Biological Station, Nanaimo, B.C. Eggs were fertilized by the dry method and incubated in the dark in vertically stacked trays until they reached the desired stage of development. Most eggs were incubated continuously at 10°C. However, some eggs were incubated at 5°C until 5 d prior to testing when they were transferred to 10°C to allow for acclimation to the test temperature (10°C). Water velocities during incubation were about 500 cm/h and dissolved oxygen (DO) levels were in excess of 90% of air saturation.

Static bioassays were conducted at 10.0 ± 0.1°C in subdued light in a series of covered 40-L fiberglass aquaria. Eggs or alevins were placed in holding chambers consisting of 50-mm lengths of 105-mm ID polyvinylchloride pipe covered at both ends by fiberglass screening. The holding chambers were positioned on screens suspended at mid-depth in the aquaria. Constant aeration provided a flow of water through the holding chambers and maintained DO levels of >95% air saturation.

Dilution water originated from the Nanaimo municipal water supply and was dechlorinated by charcoal filtration prior to use. Selected characteristics of the dilution water were total alkalinity (as $CaCO_3$) 9 mg/L, total hardness (as $CaCO_3$) 11.4 mg/L, conductance (μmhos/cm) 29.1, sodium 1.2 mg/L, calcium 3.7 mg/L, sulfate 2.9 mg/L, and chloride 2.8 mg/L. The pH of water in control aquaria varied between 7.1 and 7.3.

Water in the test aquaria was adjusted to the desired pH level with 2% reagent grade sulfuric acid. Between 8 and 13 pH levels, encompassing a range dependent on the stage and species involved, were used in each bioassay. Nominal levels were spaced at 0.1 pH unit intervals between pH 3.1 and 4.1 and at 0.2 pH unit intervals between pH 4.1 and 5.7. In addition, nominal levels of pH 6.0 and 7.3 (control) were used. Levels of pH were measured once a day using a Fisher Accumet model 320 pH meter with glass and calomel reference electrodes. Potassium acid phthalate pH 4.01 buffer was used for calibration. Levels of pH tended to rise during tests as a result of base loss from the fish (Ultsch et al. 1981). Levels were readjusted if the increase was greater than 0.02 pH units at the time of inspection.

Experimental Procedure and Statistics

Ten individuals of the species and stage to be tested were placed in each holding chamber. The holding chambers were then distributed randomly among the test aquaria to provide three chambers for a total of 30 individuals at each pH level. The toxicity tests continued for 10 d (240 h), or until all individuals had died. Holding chambers were examined for mortalities twice the 1st day (12 h and 24 h) and then once a day until the tests were completed. Dead individuals were removed at each inspection. Criteria for death were a whitening of the embryo or yolk in the eggs and the cessation of heartbeat in the alevins.

Mean pH values, calculated using equivalent hydrogen ion concentrations, were used in the analysis of the toxicity data.

Median resistance times were obtained by inspection of plots of probit percent mortality versus log time (Bliss 1937). Resistance curves were constructed as described by Sprague (1969) and equality of slopes and elevations tested by analysis of covariance.

Ten-day LC50s, LC10s, 95% confidence intervals, and slope functions were determined by probit analysis using the nomogram method of Litchfield and Wilcoxon (1949). Percent mortality at the various pH levels was normalized to 0% for controls using Abbott's formula (Finney 1952). Differences between LC50s, LC10s, and slope functions were tested at the 5% level of significance using the standard error of the difference (Litchfield and Wilcoxon 1949).

The arcsin test statistic (Sokal and Rohlf 1969) was used to test individual pH levels for mortality in excess of that in the control.

Results

Mean pH values during all the tests were within 0.1 pH unit of the desired level. Fluctuations in pH tended to be greater at higher ambient levels. Coefficients of variation averaged 4.0, 4.2, 8.9, 21.4, and 21.4%, respectively, at nominal pH levels of 3.5, 4.0, 4.5, 5.1, and 6.0.

Resistance Curves

Eyed embryos — Eyed embryos were highly resistant to acidified water. Levels of pH less than 3.7–3.9 were required to produce 50% mortality within the 10-d test period (Fig. 1). Incipient lethal pH levels could not be estimated as there was no evidence of the resistance curves approaching toxic thresholds. The five species could be divided into two groups on the basis of the slope of their resistance curves. Analysis of covariance indicated that the slopes of (1) pink and chum (pooled slope = 2.851 ± 0.295) were significantly

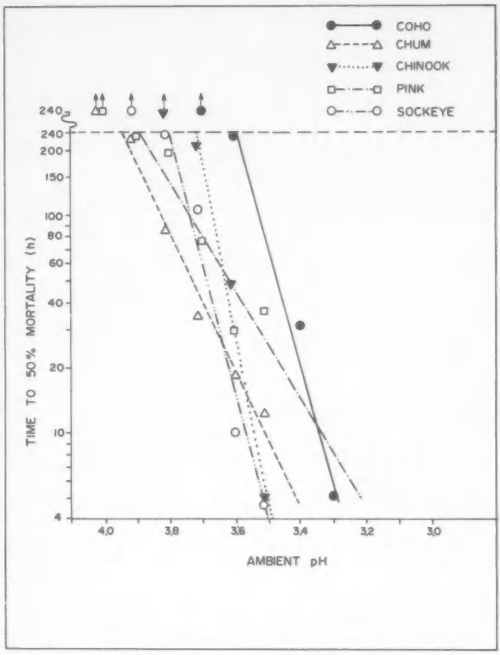

FIG. 1. Median survival times for eyed embryos of Pacific salmon exposed to low ambient pH levels.

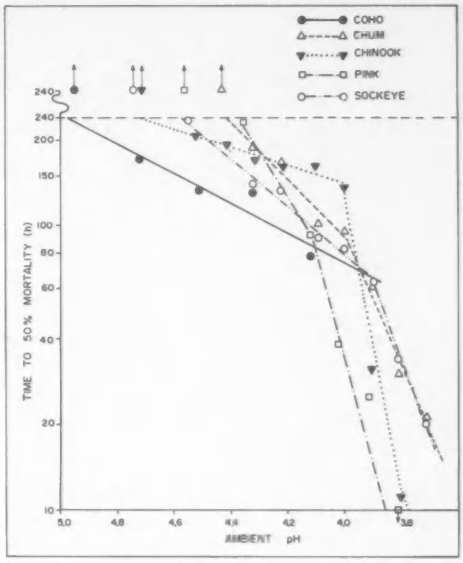

FIG. 2. Median survival times for newly hatched alevins of Pacific salmon exposed to low ambient pH levels.

less ($P < 0.001$) than those of (2) sockeye, coho, and chinook (pooled slope = 6.113 ± 0.576). This suggests some qualitative difference in the response of the two groups to the toxicant. Within each group there were quantitative differences in the acid sensitivities of the various species as indicated by significant differences ($P < 0.05$) in the elevations of the resistance curves.

Newly hatched alevins — Newly hatched alevins were more sensitive to acid than eyed embryos with 50% mortality occurring at pH levels in the range of 4.3−4.7 after 10 d (Fig. 2). As for eyed embryos, there was no indication that resistance curves for newly hatched alevins were approaching threshold levels of pH within the test period. The slopes of the resistance curves changed abruptly at pH 3.9−4.1 suggesting somewhat different modes of action for the acid at higher and lower pH levels. Analysis of covariance indicated that the slopes of the resistance curves at pH levels <4.1 were significantly greater ($P < 0.001$) than the slopes at pH levels ≥4.1. Slopes did not differ significantly among the various species at pH levels <4.1 (pooled slope = 3.378 ± 0.411), although the elevations of the curves were all significantly different ($P < 0.05$). Slopes at pH levels ≥4.1 ranged from 0.329 for chinook to 1.693 for pink. Pink and chum responded almost identically to the acid at pH levels ≥4.1 and could not be distinguished on the basis of either slope or elevation of the resistance curves. There was no

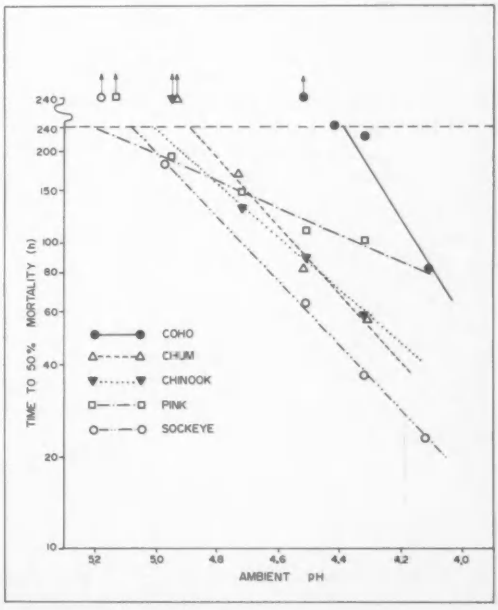

FIG. 3. Median survival times for buttoned-up alevins of Pacific salmon exposed to low ambient pH levels.

TABLE 1. Ten-day LC50 pH values for Pacific salmon embryos and alevins incubated and tested at 10°C and incubated at 5°C but tested at 10°C. The 95% confidence limits and slope functions are shown in parentheses (95% CL; S).

Species	Incubation temp. (°C)	Test temp. (C°)	Eyed embryo	Newly hatched alevin	Buttoned-up alevin
Coho	10	10	3.62(3.54−3.70; 1.45)	4.86(4.80−4.92; 1.33)	4.38(4.29−4.47; 1.78)
	5	10	3.84(3.82−3.86; 1.11)		4.49(4.39−4.59; 1.94)
Chinook	10	10	3.74(3.71−3.77; 1.15)	4.69(4.61−4.77; 1.64)	4.85(4.78−4.92; 1.53)
Sockeye	10	10	3.84(3.81−3.87; 1.25)	4.57(4.48−4.66; 1.78) 4.74(4.63−4.85; 1.62)	5.02(4.96−5.08; 1.50)
Pink	10	10	3.95(3.90−4.00; 1.39)	4.39(4.34−4.44; 1.24)	5.01(4.97−5.05; 1.33)
	5	10			5.12(5.06−5.18; 1.50)
Chum	10	10	3.93(3.87−3.99; 1.58)	4.39(4.35−4.43; 1.33)	5.00(4.92−5.08; 2.05)
	5	10		4.67(4.63−4.71; 1.19)	5.22(5.12−5.32; 2.51)

significant difference in slope between chinook and coho or between chinook and sockeye, although curve elevations were significantly different ($P < 0.01$).

Buttoned-up alevins — Toxic thresholds were not observed for any of the species in the tests with buttoned-up alevins (Fig. 3). Buttoned-up alevins were the most sensitive stage tested for all species except coho. Coho were considerably more resistant than the other species. However, the slope of the resistance curve for coho was not significantly different from the slopes for chum, sockeye, and chinook (pooled slope = 1.081 ± 0.078) suggesting that the mode of action of the acid was similar in these species. The pH level at which the acid became effective varied for the different species as indicated by significant differences ($P < 0.01$) in the elevations of the resistance curves. Pink apparently responded somewhat differently to low pH than the other species as the slope of their resistance curve (0.442) was significantly lower ($P < 0.01$) than that of the other species.

Eyed embryos and newly hatched alevins exposed to pH levels <4.1 appeared to respond similarly to the acid, as did newly hatched alevins exposed to pH levels ≥4.1 and buttoned-up alevins. Analysis of covariance indicated that there was no significant difference between the slopes of the resistance curves for (1) eyed embryos and (2) newly hatched alevins at pH levels <4.1 or between slopes for (3) newly hatched alevins at pH levels ≥4.1 and (4) buttoned-up alevins. The curve elevations for all groups were significantly different ($P < 0.01$). Differences in slope between groups (1) or (2) and groups (3) or (4) were highly significant ($P < 0.001$).

LC50 VALUES

The 10-d LC50 values varied significantly ($P < 0.01$) both with life stage and with species (Table 1). Acid sensitivity generally increased with age. Stage sensitivities (10-d LC50 pH range) were ranked buttoned-up alevins (4.38−5.22) > newly hatched alevins (4.39−4.69) > eyed embryos (3.62−3.95) for all species except coho. Coho were more sensitive as newly hatched alevins than at button-up.

The various species were ranked in order of decreasing sensitivity to low pH at each of the developmental stages. Ranking was based on significant differences ($P < 0.05$) in LC50 values. Eyed embryos were ranked (pink, chum) > sockeye > chinook > coho, newly hatched alevins were ranked coho > (sockeye, chinook) > (pink, chum), and buttoned-up alevins were ranked (chum, pink, sockeye) > chinook > coho.

Embryos and alevins incubated at 5°C but tested at 10°C were more sensitive to low pH than embryos and alevins at the same ontogenetic stage incubated and tested at 10°C. LC50 values were higher for the fish incubated at 5°C in all six cases, and significantly higher ($P < 0.05$) in four of the six cases, where comparisons were made.

The mean slope function (95% confidence limits) of the probit mortality plots for all tests was 1.49 (1.38−1.60). Slope functions did not vary significantly with stage, species, or incubation temperature.

LC10 VALUES

Ten-day LC10s for eyed embryos ranged from pH 3.82 for chinook to pH 4.19 for chum. LC10s for the most sensitive alevin stage of each species ranged from pH 5.01 for coho to pH 5.74 for chum (Fig. 4). There was close agreement between the LC10 value calculated for each bioassay and the actual least acidic pH level tested that resulted in significant mortality.

Abnormal behavior was noted at sublethal pH levels only among buttoned-up alevins of pink and chum. When compared to alevins held at pH 7.3, many of the buttoned-up pink and chum held at pH 6.0−6.1 appeared lethargic if left undisturbed. However, if they were agitated by some external stimulus such as light or the movement of a nearby object, they became hyperactive and did not swim in a fully coordinated manner.

Discussion

Fish populations usually disappear from acidified waters as a result of recruitment failure (Jensen and Snekvik 1972; Beamish et al. 1975; Rosseland et al. 1980). Laboratory experiments indicate that oogenesis (Mount 1973; Craig and Baksi 1977; Ruby et al. 1977) and embryonic and larval development (Krishna 1953; Johansson and Kehlstrom 1973;

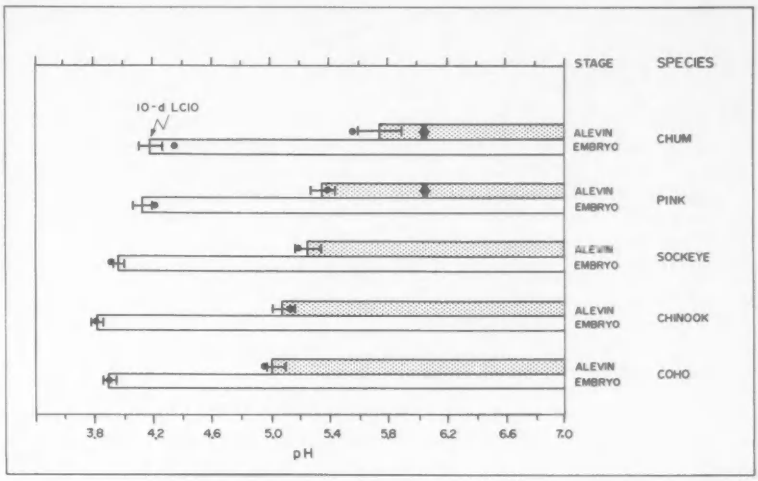

FIG. 4. Highest acutely lethal acid pH levels for eyed embryos and the more sensitive of the two alevin stages tested for the five species of Pacific salmon. Bar graphs indicate 10-d LC10s and 95% confidence limits. Closed circles indicate actual highest acid pH tested that caused significant mortality. Diamond marks indicate highest pH levels at which behavioral abnormalities were observed in alevins.

Trojnar 1977; Daye and Garside 1977, 1979) are particularly sensitive to low pH. There is some controversy as to which process is the more sensitive and therefore responsible for reproductive failure in natural populations (Lee and Gerking 1980). Extensive field studies in Norway seem to indicate that high embryo and alevin mortality rather than the failure of egg deposition is largely responsible for the disappearance of salmonid populations (Jensen and Snekvik 1972; Amundsen and Lunder 1974; Rosseland et al. 1980; SNSF 1980). However, there is recent evidence that acid exposure may affect oogenesis adversely but that this may not become apparent until later during embryonic development (Kennedy 1980). The greatest potential impact of acid pH on anadromous stocks of Pacific salmon is probably on early survival as oogenesis is largely complete by the time prespawning adults enter fresh water. Interference with normal oogenesis may be important in nonanadromous stocks.

STAGE SENSITIVITY

Eyed embryos of all five species of Pacific salmon were more resistant to low pH than either newly hatched or buttoned-up alevins. Eyed embryos also were more resistant to low pH than alevins in Atlantic salmon, *Salmo salar* (Daye and Garside 1977, 1979; Daye 1980), rainbow trout, *Salmo gairdneri* (Daye 1980; Gunn and Keller 1980), brown trout, *Salmo trutta* (Brown and Lynam 1981), and brook trout, *Salvelinus fontinalis* (Menendez 1976). The greater resistance of eyed embryos has been attributed to the ability of the zona radiata (capsule) to sequester H^+ ions and to the buffering capacity of the perivitelline fluid (Daye and Garside 1977, 1980; Johansson et al. 1977). Direct measurements indicate that the pH of the perivitelline fluid is between 0.4 and 0.8 pH units above ambient levels in eggs exposed to acid waters in the range of pH 4.0–5.0 (Johansson et al. 1977; Peterson et al. 1980). The loss of the zona radiata at hatch effectively exposes the newly hatched alevin to a more acidic environment and results in mortality at higher ambient levels even though the inherent sensitivity of the organism may have changed little.

The relatively low levels of pH tolerated at the eyed stage probably overestimate the ability of Pacific salmon embryos to develop normally in acid waters. Acute toxicity tests indicated that embryos were more sensitive during cleavage than at the eyed stage in both Atlantic salmon (Daye and Garside 1977; Daye 1980) and brown trout (Brown and Lynam 1981). Chronic tests showed that the incipient lethal level for Atlantic salmon embryos was determined primarily during cleavage and gastrulation (Daye and Garside 1979). Pacific salmon embryos probably also are more sensitive during cleavage and gastrulation than at the eyed stage, and it is essential that these early stages be tested before setting criteria for safe levels of acid pH during embryonic development.

Grande et al. (1978) suggested that there was a tendency in salmonids for acid tolerance to decrease with age during the alevin–fry stages. In the current study, buttoned-up alevins were significantly more sensitive to low pH than newly hatched alevins in four of the five species of Pacific salmon. Older alevins also appeared more sensitive in Atlantic salmon (Daye and Garside 1977; 1979). However, the decrease in acid sensitivity between hatch and button-up in coho indicates the necessity of examining each species individually.

The increase in acid sensitivity in most species between hatch and button-up probably is a consequence of gill development and the shift in the main site of ion and gas exchange from the relatively robust integument to the more fragile

branchial epithelium. Daye and Garside (1980) observed that the integument was the primary site of injury in Atlantic salmon embryos and early alevins exposed to low pH. However, as the gills expanded in later alevins they became the main site of tissue destruction.

Embryos and alevins of Pacific salmon were more sensitive to low pH if they were incubated at 5°C but tested at 10°C than if they were incubated and tested at 10°C. This effect was not abolished by transferring the fish incubated at 5°C to the test temperature 5 d before they were to be tested. Kwain (1975) reported that rainbow trout embryos were more sensitive to low pH at 5°C than at 10°C. He attributed the greater sensitivity of embryos at 5°C to a longer incubation period and hence to a longer period of exposure to the acid. This was obviously not the case for the Pacific salmon as the period of exposure was the same regardless of the incubation temperature. It is unlikely that the difference in the sensitivity of Pacific salmon incubated at 5 and 10°C was simply the result of having tested different ontogenetic stages as care was taken to ensure that identical stages were selected for all tests. A more probable explanation is that the metabolic changes associated with acclimation to one temperature adversely affect the ability of fish to tolerate low pH at another temperature.

Relative Species Sensitivity

The relative sensitivities of the various species of Pacific salmon to low pH were dependent on the stage of development. Species were ranked (chum, pink) > sockeye > chinook > coho in order of decreasing acid sensitivity as eyed embryos but coho > (chinook, sockeye) > (pink, chum) as newly hatched alevins and (chum, pink, sockeye) > chinook > coho as buttoned-up alevins.

The ranked order for newly hatched alevins was almost the exact opposite of that for eyed embryos. It is unlikely that this was the result of profound physiological differences between the two stages as there was at most only 5 d between the start of the tests with newly hatched alevins and the end of the tests with eyed embryos. It is more probable that the difference in relative sensitivities occurred because the newly hatched alevins were exposed directly to the acid whereas the eyed embryos were shielded by the zona radiata and perivitelline fluid. A major factor influencing the relative sensitivities of other salmonid embryos appears to be differences in the buffering capacity of the perivitelline fluid. Johansson et al. (1977) observed that Atlantic salmon, which were more sensitive than brown trout, had a perivitelline fluid pH about 0.4 units lower than that of brown trout exposed to the same ambient pH level. Similar interspecific differences in the buffering capacities of the perivitelline fluid probably played an important role in determining the relative acid sensitivities of eyed embryos of Pacific salmon. In contrast, the sensitivities of the newly hatched alevins depended only on the inherent physiological capacity of each species to resist the stress caused by low pH.

Interspecific differences in the acid sensitivities of both newly hatched alevins and buttoned-up alevins probably reflected differences in the ionoregulatory and osmoregulatory capacities of the various species as ionoregulatory failure is the primary cause of death at moderately acidic pH levels (Haines 1981). The difference in the ranked orders for the newly hatched alevins and for the buttoned-up alevins appears to be largely the result of major changes in the hypo-osmotic regulatory capacities of pink and chum. Both species normally migrate to sea as fry and undergo preadaptive physiological changes during yolk absorption in anticipation of entering the marine environment (Weisbart 1968; Kashwagi and Sato 1969). These changes have been shown to impair the ability of alevins to regulate hydromineral balance in hypotonic solutions (Iwata et al. 1982). As a result pink and chum are particularly susceptible near button-up to ionic disturbances such as those caused by excess hydrogen ion.

Comparison with Other Salmonids

The range of pH values reported in the literature as having caused significant mortality among embryos and alevins of a given salmonid species is often very broad. For example, incipient lethal levels as high as pH 6.1 (Menendez 1976) and as low as pH 4.0 (Trojnar 1977) have been reported for brook trout. This broad range occurs partly because acid toxicity is a complex phenomenon dependent on variables such as water hardness (Gunn and Keller 1980; Brown and Lynann 1981; Nelson 1982), type of acid (Graham and Wood 1981), temperature (Kwain 1975), acclimation pH (Trojnar 1977), parental exposure (Menendez 1976), strain difference (Johansson et al. 1977; Swarts et al. 1978), and stage of development (Daye and Garside 1977). However, much of the variation occurs because of differences in experimental design and the statistical end point reported. This makes it difficult to compare species in terms of their sensitivity to low pH on the basis of lethal values reported by different investigators. Fortunately, a few studies have examined the acid sensitivities of embryos or alevins of several salmonid species under the same experimental conditions (Bua and Snekvik 1972; Johansson et al. 1977; Grande et al. 1978) and it is possible to provide a general ranking for some of the more common species. These studies indicate the following ranking in order of decreasing sensitivity to low pH: rainbow trout (*Salmo gairdneri*) > lake trout (*Salvelinus namaycush*) > Atlantic salmon (*Salmo salar*) > brown trout (*Salmo trutta*) > brook trout (*Salvelinus fontinalis*).

I attempted to estimate the sensitivities of the Pacific salmon in relation to other salmonids by comparing the results obtained in the current study with those reported for other species in previous studies. However, the only study in which the experimental design and conditions were similar enough to those in the current study to allow valid comparisons of acid sensitivity was that of Daye (1980). Daye (1980) reported a 7-d LC50 of pH 4.3−4.4 for rainbow trout alevins 2 wk after hatch and a 7-d LC50 of pH 4.1−4.4 for Atlantic salmon alevins near button-up. Both species were tested in soft water (11.4 mg/L as $CaCO_3$) at 8°C. Seven-day LC50s were estimated for newly hatched and buttoned-up alevins of the Pacific salmon from the resistance curves in Fig. 2 and 3. The range of the 7-d LC50s (pH 4.2−4.4) for newly hatched Pacific salmon, excluding coho, was almost identical with that for rainbow trout indicating similar sensitivities to low

pH. The 7-d LC50 (pH 4.7) for newly hatched coho was greater than the value reported for rainbow trout suggesting a greater acid sensitivity for coho. However, this comparison considerably overestimates the overall sensitivity of coho alevins because the acid sensitivity of coho decreased with age whereas the sensitivities of the other species increased with age. The relatively low overall sensitivity of coho is apparent in the comparison with Atlantic salmon. The 7-d LC50 (pH 4.3) for coho was about the same as that for Atlantic salmon whereas the LC50 values (pH range 4.75−4.95) for the other species were considerably higher. On the basis of these comparisons, a tentative ranking would place coho between Atlantic salmon and rainbow trout and chum, pink, sockeye, and chinook roughly equivalent to rainbow trout in their sensitivity to low pH. This ranking emphasizes the high sensitivity of the Pacific salmon as rainbow trout was the most sensitive salmonid species previously tested for its ability to tolerate acid pHs.

Implications of Low pH for Pacific Salmon

The Pacific salmon appear to be more sensitive to low pH than most other salmonids. My study indicates that 10-d LC10s for alevins of the various species ranged between pH 5.01 and 5.74. However, there was no indication that acute mortality had ceased after 10 d in any of the species and significant mortality would be expected at higher pH levels than those reported with a longer exposure period. Chum and pink appear to be particularly sensitive as under natural conditions the abnormal behavior noted at pH 6.0 probably would have resulted in significant mortality as a result of predation or failure to obtain adequate food. Longer term studies are needed to determine precise limits of acid tolerance but it is clear that the Pacific salmon, with a possible exception of coho, can tolerate only relatively minor depressions from neutrality in ambient pH without detrimental effects.

The apparent global trend toward more acidic precipitation may have serious implications for the Pacific salmon. Their high sensitivity to low pH severely limits the prospects of establishing self-sustaining populations in those regions of eastern North America and western Europe that have already experienced significant acidification of surface waters. Although it is not generally recognized, there also are reasons to be concerned about the potential impact of acid pH on Pacific salmon in areas of western North America. Much of western North America has a bedrock geology considered conducive to surface water acidification (Anon. 1981). The precipitation over the more densely populated areas of southwestern British Columbia and Washington State currently has a mean annual pH in the range of 4.5−5.0, and because of the high rainfall this results in a very high annual deposition of H^+ (Anon. 1981; Rubec 1981). Many of the waters in this area are extremely soft (total hardness <10 mg/L and $CaCO_3$) and are thus vulnerable to acidification. Levels of pH as low as 5.3 have been recorded at the Chehalis River Hatchery near Vancouver, B.C., and levels in the range of pH 5.8−6.2 have been recorded at a number of other salmonid enhancement sites in the region (D. D. MacKinlay, Department of Fisheries and Oceans, 1090 W. Pender St., Vancouver, B.C., personal communication). These levels are close to, or within, the pH range I found to have a significant adverse effect on salmon alevins in the laboratory. There is circumstantial evidence that these relatively low pH levels may be causing problems (mortality, poor growth, abnormal behavior) at some hatcheries (B. Anderson, Department of Fisheries and Oceans, 1090 W. Pender St., Vancouver, B.C., personal communication) but more information is required before this can be substantiated. Reliable indicators of chronic acid stress would be particularly useful in this regard. Leivestad and Muniz (1976) were able to correlate reduced plasma sodium and chloride concentrations with acid stress in juvenile and adult brown trout both in the laboratory and in the field. If similar indicators of acid stress can be found for alevins and fry of Pacific salmon, it should be possible to establish whether the problems associated with low pH levels at the hatcheries are in fact the result of acid stress. Confirmation that acid stress is involved would indicate that there are indeed reasons to be concerned about the potential acidification of surface waters in at least some areas of western North America.

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Effects of Hypoxia and Surface Access on Growth, Mortality, and Behavior of Juvenile Guppies, *Poecilia reticulata*

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WEBER, J.-M., AND D. L. KRAMER. 1983. Effects of hypoxia and surface access on growth, mortality, and behavior of juvenile guppies, *Poecilia reticulata*. Can. J. Fish. Aquat. Sci. 40: 1583–1588.

Juvenile guppies (*Poecilia reticulata*) were fed ad libitum and maintained for 11 d at oxygen concentrations ranging from 0.5 to 8 mg/L (25–26°C). With access to the surface, guppies showed high growth rates and low mortality at all concentrations. Without surface access, they exhibited a progressive reduction in growth rate below 2–3 mg/L and did not survive below 1 mg/L. Activity was influenced by oxygen concentration and surface access. Feeding rates declined sharply with oxygen concentration for fish without surface access and to a lesser extent for fish with access. Percent time in contact with the surface increased as oxygen decreased. Aquatic surface respiration is used even when this behavior is not necessary for survival. We suggest that aquatic surface respiration increases the energy available for growth under hypoxic conditions by augmenting oxygen supply, which permits greater ingestion rate, and possibly by decreasing the cost of ventilation.

WEBER, J.-M., AND D. L. KRAMER. 1983. Effects of hypoxia and surface access on growth, mortality, and behavior of juvenile guppies, *Poecilia reticulata*. Can. J. Fish. Aquat. Sci. 40: 1583–1588.

Des guppies juvéniles ont été nourris *ad libitum* et gardés pendant 11 jours à des concentrations en oxygène allant de 0,5 à 8 mg/L (25–26°C). Lorsqu'ils avaient accès à la surface, les guppies montrèrent des taux de croissance élevés et une faible mortalité à toutes les concentrations. Sans accès à la surface, leurs taux de croissance furent progressivement réduits au-dessous de 2–3 mg/L et ils ne survécurent pas à moins de 1 mg/L. L'activité fut influencée par la concentration en oxygène et l'accès à la surface. Les taux d'alimentation diminuèrent rapidement avec la concentration en oxygène pour les poissons sans accès à la surface et, à un degré moindre, pour les poissons y ayant accès. Le pourcentage du temps total passé en contact avec la surface augmenta à mesure que diminuait l'oxygène. La respiration aquatique de surface est utilisée même quand ce comportement n'est pas nécessaire à la survie. Nous suggérons que la respiration aquatique de surface augmente l'énergie disponible pour la croissance lorsque les conditions sont hypoxiques, en accroissant l'apport d'oxygène, ce qui permet un plus grand taux d'ingestion, et peut-être en diminuant le coût de la ventilation.

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BECAUSE oxygen depletion occurs in many aquatic habitats, the effects of hypoxia on fish have been the subject of considerable research. Lethal limits, metabolic rate, and other physiological or behavioral responses to low oxygen concentration have been well studied (Doudoroff and Shumway 1970; Petit 1973; Davis 1975), but growth has received much less attention. Growth should be a valuable indicator of the consequences of hypoxia because it is an integrated measure of the complex pathways involved in the procurement, processing, and expenditure of energy by the organism. Studies to date suggest that oxygen acts as a limiting factor for growth, with a threshold between 4 and 5 mg/L for several species (Brett and Blackburn 1981). However, these studies have largely ignored the potential importance of surface access. When oxygen depletion occurs in the water column, many fishes use the thin, well-oxygenated surface layer to ventilate their gills (Lewis 1970; Gee et al. 1978; Kramer and McClure 1982). By augmenting the oxygen concentration of inspired water, this should increase oxygen uptake rate and/or decrease the work of ventilation as compared to subsurface respiration. Surface access is known to favor survival (Lewis 1970; Kramer and Mehegan 1981; Kramer and McClure 1982), to allow maintenance of high arterial pO_2 (Burggren 1982), and to prevent depletion of muscle adenylates (Vetter and Hodson 1982). In this study, we examined its effect on growth. In an attempt to understand better the mechanisms by which surface access and oxygen concentration determine growth rate, we

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measured activity, feeding rate, and percent time spent at the surface. The guppy, *Poecilia reticulata*, was chosen as a test species. It is native to Trinidad and northeastern South America where it can be found in habitats ranging from well-oxygenated streams to stagnant pools, with oxygen concentrations as low as 0.3 mg/L (Weber unpublished observations).

Materials and Methods

Adult guppies collected in May 1980 from El Cedro River (24.5°C), Trinidad, West Indies (tributary of Guanapo River, Northern Mountain Range), were maintained at 25−26°C, with a 12-h artificial light photoperiod (08:00−20:00), supplemented and extended by natural light from windows. Two hundred young were obtained from a brood stock of ~50 adults. The young were kept in a well-aerated 180-L tank and fed presoaked, finely ground TetraMin, carefully deposited on the substrate, to avoid habituation to surface feeding and to simulate natural foraging conditions (see Dussault and Kramer 1981). At the start of the experiment, fish were 21 ± 2 d old.

Six oxygen concentrations were selected: 0.5, 1.0, 1.5, 2.0, 3.0, and 8.0 mg/L. Attention was focused below 3 mg/L for three reasons: (1) Adults initiate aquatic surface respiration at about 2.5 mg/L (Kramer and Mehegan 1981). (2) In preliminary experiments, growth was not affected at 2 mg/L when guppies could reach the surface. (3) The incipient lethal level is close to 1 mg/L when guppies are deprived of surface access (Weber unpublished observation).

Two groups of fish were tested in a double Plexiglas chamber at each oxygen concentration. One group had free access to the surface, the other was prevented from reaching it, but the water circulated through both sections. Oxygen concentrations were adjusted in six 40-L tanks, in which the Plexiglas chambers were suspended. Each tank contained a mixing device to distribute dissolved gases evenly. This device was tested with dyes and found to circulate water adequately throughout the space not occupied by the chamber. All tanks except the one at saturation were placed in series with two 22-L glass bottles forming a closed-circuit system through which water was continuously pumped at 600 mL/min. Deoxygenation was accomplished by bubbling nitrogen through the bottles. Progressive reoxygenation was performed along the circuit. The desired concentrations were finely adjusted in each tank by bubbling only nitrogen (0.5 mg/L), mixtures of nitrogen and air (1.0, 1.5, and 2.0 mg/L), or air alone (3.0 mg/L) through the mixing devices. The sixth tank was kept at oxygen saturation in a separate closed-circuit system with a 9-L header tank. The volume of water per fish as well as the circulation flow rate were identical in the two systems and 10% of the water was renewed daily.

Oxygen concentration and temperature were measured every 2 h (09:00−17:00) with an oxygen electrode and meter (Yellow Springs Instruments Co., model 57). Calibration was checked by the Winkler method and found accurate within 0.1 mg/L. Readings were taken separately in the two compartments forming each double chamber. A Plexiglas tube was introduced into the compartment to pump water out past the electrode and back to its original location. Even though the fish were habituated to the sampling device, no behavioral measurement was taken less than 30 min after an oxygen reading. Actual oxygen concentrations during the experiment averaged within 6% of the target values with SE of no more than 3% of the means ($n = 50$). The variance of the first daily oxygen readings was equal to the variance of all the measurements, indicating that the nocturnal fluctuations were probably not exceeding the ones measured during the day. In the 0.5 mg/L treatment without surface access, 100% mortality occurred during the deoxygenation period before the target value was reached.

Before the determination of initial and final wet weights, fish were deprived of food for 24 h to empty their digestive tracts. They were blotted on a wet paper towel and weighed to the nearest milligram, in water without anesthetic. Dry weights (±0.1 mg) were obtained after killing the fish in an ice bath and desiccating them for 24 h at 60°C. At the beginning of the experiment a separate group of 30 fish from the same batch was killed to determine the conversion factor between initial wet and dry weights. Initial dry weight was measured as 21.3% (SE = 0.53) of the initial wet weight. This value was used for the back calculation of initial dry weights of the test fish. At each oxygen concentration the variance of the initial weights was low (Table 1) and the mean initial weight was used as initial weight of all the fish of that group in the calculation of their growth rate. This commonly used procedure (Stewart et al. 1967; Brett and Blackburn 1981) is an unbiased way to obtain confidence limits around the mean growth rates when it is not possible to mark fish individually. Specific growth rates in dry weight were calculated (Ricker 1979). A two-dimensional index of activity was obtained by observing eight randomly chosen individuals for 1 min each, using a grid of sixteen 4 × 4 cm squares on the front of the chamber. The numbers of vertical and horizontal lines crossed were recorded separately with a cumulative counter.

Pecking rate (Dussault and Kramer 1981), used as an index of feeding rate, was measured simultaneously with activity. One peck was defined as a rapid movement towards and away from the substrate. To measure aquatic surface respiration, the number of fish touching the surface was counted every 10 s for a period of 2 min. For each 2-min observation, the mean was divided by the total number of fish present. Before the experiment, fish were randomly divided into 12 groups of ~15 individuals and placed in the chambers for 1 wk. During this period, they were fed ad libitum and kept at normoxia. Initial weights were measured at day 0. On day 1, oxygen concentrations were adjusted to the desired levels over a 3-h period. Activity and feeding were recorded from all chambers in random order every 2nd day starting on day 2. Percent time in contact with the surface was recorded in random order daily starting on day 1. Fish were killed after 10 d at the prescribed oxygen levels.

Presoaked TetraMin was fed to the fish on the gravel substrate of the chambers daily. The amount was equal to 20% of the initial wet weight of the fish, increased throughout the experiment on the basis of estimated weight increments. Remaining food and excrements from the day before were siphoned out early in the morning before feeding. No algal growth was observed in the chambers.

TABLE 1. Weights and growth rates of juvenile guppies raised for 11 d at six oxygen concentrations, with and without access to the surface. Temperature 25–26°C. Mean ± SE, sample size (n). Mortality can be determined by the change in sample size between initial and final weights. (—) indicates where 100% mortality occurred.

	Target O_2 (mg/L)	Initial wet weight (mg)	Calculated initial dry weight (mg)	Final wet weight (mg)	Final dry weight (mg)	Specific growth rate (% dry weight/d)
No access to the surface	0.5	14.07±0.88 (15)	3.00±0.23	—	—	—
	1.0	14.13±1.23 (15)	3.03±0.33	17.18±1.17 (11)	4.02±0.28	2.34±0.66
	1.5	13.27±0.57 (15)	2.81±0.15	19.50±1.13 (10)	4.17±0.27	3.41±0.62
	2.0	13.07±1.16 (14)	2.74±0.31	23.00±1.75 (9)	4.86±0.62	4.62±1.15
	3.0	13.27±1.29 (15)	2.78±0.35	23.46±1.73 (13)	5.48±0.46	5.71±0.87
	8.0	13.33±0.61 (14)	2.83±0.16	22.62±1.45 (13)	5.24±0.44	5.16±0.84
Access to the surface	0.5	14.33±1.19 (15)	3.11±0.32	23.64±2.22 (14)	5.62±0.62	4.70±0.97
	1.0	13.20±1.20 (15)	2.77±0.32	23.00±1.73 (13)	5.31±0.48	5.46±0.83
	1.5	13.80±1.19 (13)	2.93±0.33	26.33±2.97 (9)	6.16±0.83	5.91±1.47
	2.0	15.53±1.38 (15)	3.41±0.37	25.87±1.96 (15)	6.18±0.59	4.48±0.95
	3.0	14.07±1.13 (15)	3.01±0.31	25.69±2.07 (13)	6.32±0.62	6.16±0.97
	8.0	12.93±1.10 (15)	2.69±0.30	23.85±2.35 (13)	5.64±0.70	5.81±1.23

Statistical analyses were performed using the Statistical Analysis System (SAS 1979).

Results

Oxygen had no effect on mortality, which averaged 12% (Table 1) when guppies had access to the surface. However, when access was prevented at 0.5 mg/L, mortality reached 100% within 2–4 h. This mortality was significantly higher than at all other oxygen concentrations ($P < 0.005$, Fisher Exact Probability Test). Comparisons of fish with and without access to the surface showed that mortality was generally higher without access and significantly higher at 0.5 mg/L ($P < 0.005$) and at 2 mg/L ($P < 0.05$).

Initial weights were not different among the 12 groups of 15 fish ($F = 0.44$, $P > 0.75$, ANOVA, SAS GLM procedure). When the fish were allowed to reach the surface, their growth rate was independent of oxygen concentration ($F = 0.44$, $P = 0.82$, ANOVA), and was close to 5% per day at all concentrations (Table 1). When juvenile guppies were prevented from reaching the surface, oxygen had a significant effect on their growth rate ($F = 2.72$, $P < 0.05$), which was sharply reduced below 2 mg/L with a threshold concentration between 2 and 3 mg/L. Paired comparisons for each oxygen concentration showed that the effect of surface access on growth rate was only significant at 1.0 mg/L ($P < 0.01$, t-test).

Horizontal activity was always greater than vertical activity (Fig. 1). At normoxia activity was similar for fish with and without access to the surface. When guppies had access to the surface horizontal activity increased progressively with hypoxia, approximately doubling at 0.5 mg/L, compared to normoxia. Vertical activity also increased, reaching ~3 times the value measured at normoxia. When prevented from reaching the surface, the activity of guppies changed only slightly in response to oxygen. However, there was a significant decrease in vertical activity below 1.5 mg/L ($F = 3.95$, $P < 0.005$, nonparametric ANOVA, SAS NPAR1WAY procedure). To investigate the effects of oxygen and surface access, activity data were analyzed with a 2-way ANOVA. Variances were stabilized by empirical power transformation (Taylor 1961) to meet the assumptions of ANOVA. Although the distribution remained different from normal, the conclusions were not affected as all the F-ratios were large (Box and Andersen 1954). Oxygen, access to the surface, and

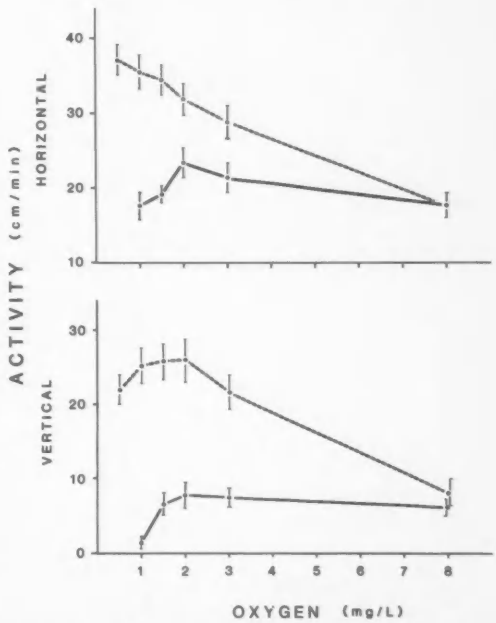

FIG. 1. Mean levels of horizontal and vertical activity (±SE, $n = 40$) of juvenile guppies. Fish with access to the surface (broken line), and without access (solid line). Note that the ordinate for horizontal activity does not start at 0.

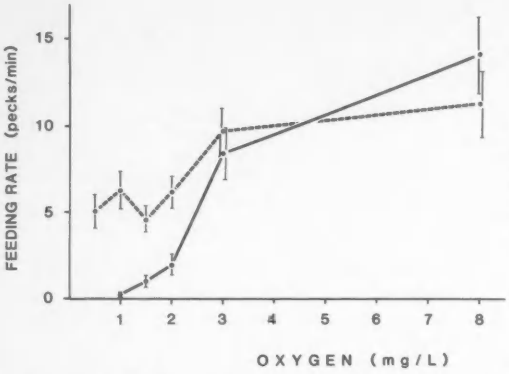

FIG. 2. Mean feeding rates (±SE, $n = 40$) of juvenile guppies in relation to oxygen concentration. Fish with access to the surface (broken line), and without access (solid line).

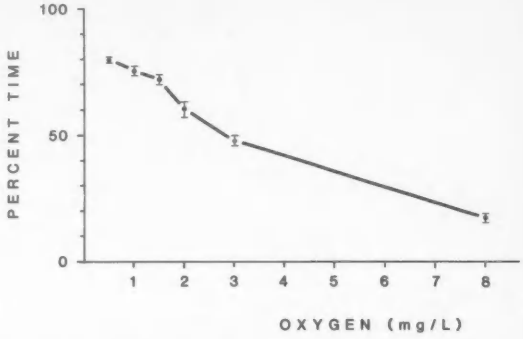

FIG. 3. Mean percent time in contact with the surface (±SE, $n = 20$) in relation to oxygen concentration, for juvenile guppies.

their interaction all had highly significant effects on activity ($P < 0.001$). Results were generally similar for horizontal and vertical activity. However, surface access had a much stronger effect on vertical than on horizontal activity (F-value about five times greater for vertical activity).

Pecking rate was progressively reduced with increased hypoxia, with the major decline occurring below 3 mg/L (Fig. 2). The effect of hypoxia was greater when fish did not have access to the surface ($F = 24.22$, $P < 0.0001$, nonparametric ANOVA), than when they did have access ($F = 4.86$, $P = 0.0003$). The overall effect of surface access was highly significant ($Z = 5.40$, $P < 0.0001$, Wilcoxon 2-sample test).

Percent time at the surface (Fig. 3) increased with hypoxia ($F = 130.9$, $P < 0.0001$, nonparametric ANOVA). At all concentrations except at saturation, percent time at the surface decreased throughout the 11-d experiment [significant slopes = (−1.48) to (−3.17), $r^2 = 0.54-0.86$, $P < 0.01$, linear regressions after arcsine transformation].

Discussion

In juvenile guppies prevented from reaching the surface, oxygen acted as a limiting factor for growth as in previously studied species. The oxygen threshold for growth between 2 and 3 mg/L is about 2 mg/L lower than the threshold of 4−5 mg/L found in all other well-documented species (Brett and Blackburn 1981). These species include not only the salmonids: coho salmon, *Oncorhynchus kisutch*, and sockeye salmon, *O. nerka*; and the largemouth bass *Micropterus salmoides* (Stewart et al. 1967), but also the common carp *Cyprinus carpio* (Chiba 1966), a fish resistant to hypoxia (Lomholt and Johanssen 1979). Pike, which have also a high tolerance for hypoxia (Adelman and Smith 1970; Casselman 1978), may have a threshold between 3 and 4 mg/L, but the evidence presented by Adelman and Smith (1970) is based on small sample sizes, and a precise threshold value is difficult to determine. Brett (1979) has noted that the oxygen threshold for growth may be lowered if fish are fed less than the maximum ration. The low threshold found in the present study was not due to insufficient feeding. Food was always available and the growth rate measured at normoxia (5% dry weight per day) was high and similar to maximum growth rates for guppies fed dried food ad libitum in other studies (Dussault and Kramer 1981).

Without access to the surface, oxygen concentrations of 0.5 mg/L were insufficient to sustain life, but most fish survived at 1.0 mg/L. Lethal limits are above 1.5 mg/L in many species (Doudoroff and Shumway 1970). Thus, even without surface access, the guppy is physiologically resistant to hypoxia. When access to the surface was permitted, both the lethal effect and the growth-reducing effect of hypoxia were eliminated. This study provides the first evidence that surface access can have an effect on the relationship between oxygen concentration and fish growth. Previous investigations had demonstrated a short-term survival advantage of surface access (Lewis 1970; Kramer and Mehegan 1981). Here, we document an advantage over an 11-d period during which guppies with access to the surface were able to survive at an oxygen concentration as low as 0.5 mg/L. Some previous studies of the effects of hypoxia on mortality (Doudoroff and Shumway 1970) and on growth (Brett and Blackburn 1981) allowed access to the surface; others did not. Consideration of surface access in determining the effects of hypoxia is ecologically relevant. Studies preventing surface access may show growth reductions which would not occur in natural habitats where fish can normally reach the surface. On the other hand, surface access may be restricted in some habitats because of ice cover, floating vegetation, large travel distances, intense aerial predation, or inability to cross the thermocline. Guppies spent a greater proportion of their time at the surface when oxygen concentration was lower. The strong negative correlation between oxygen concentration and percent time spent at the surface indicates that guppies may extract a greater proportion of their total oxygen uptake from the surface layer as oxygen concentration is reduced in the water column. Without surface access, total oxygen uptake is probably reduced and/or more energy is expended for ventilation. Except at saturation, percent time spent at the surface decreased throughout the experiment. This was probably not

an effect of size since Kramer and Mehegan (1981) showed that aquatic surface respiration increases with size in adult guppies. Fish may have acclimated to hypoxia, progressively reducing their oxygen needs or increasing their uptake efficiency over the 11 d. The benefits of aquatic surface respiration may be larger for guppies because their small size, flattened head, and upturned mouth favor exploitation of the surface layer (Lewis 1970; Kramer and Mehegan 1981). Some physiological tolerance to hypoxia may always be linked with the ability to perform aquatic surface respiration.

This study shows that the relationship between oxygen concentration and activity depends on surface access. Guppies with access to the surface strongly increased their horizontal activity, probably as a consequence of local oxygen depletion at the surface (Lewis 1970). Most of the horizontal movements took place at the surface where these fish spent a large proportion of their time. Fish with access to the surface almost tripled their vertical activity when oxygen declined because they repeatedly dove to the bottom to feed and came back to the surface to perform aquatic surface respiration. High activity and high percent time at the surface probably would limit the amount of time available for other activities. Low feeding rates below 3 mg/L may have been caused by this time constraint. The growth responses of fish with and without access to the surface cannot be explained by indirect effects of oxygen on activity. Fish with access were able to maintain a high growth rate even though activity increased sharply. Fish without access showed reduced growth rates below 2 mg/L, but activity stayed constant or even decreased.

Pecking rate decreased with oxygen concentration, as in previous studies of the effect of hypoxia on food consumption (Herrmann et al. 1962; Stewart et al. 1967). This study presents the first evidence that, under hypoxic conditions, fish without access have lower feeding rates than fish with access. Feeding rate of fish without access to the surface was ~3, 5, and more than 20 times lower than that of fish with access at 2.0, 1.5, and 1.0 mg/L, respectively. These differences in feeding rate may partly explain the effects of surface access and oxygen concentration on growth. Because increasing ration increases oxygen consumption (Brett and Groves 1979), it may be that fish without access eat only the quantity of food that their oxygen supply allows them to process.

In conclusion, this study shows that guppies are able to cope with hypoxia both because they are physiologically tolerant to low oxygen and because they use aquatic surface respiration. Oxygen thresholds for growth are probably more variable than indicated by the ecologically diverse but small number of temperate species investigated previously (Brett and Blackburn 1981). Aquatic surface respiration is initiated at higher oxygen concentrations than absolutely necessary for survival, and this behavior provides an energetic advantage in terms of growth. More energy may be available for growth because aquatic surface respiration increases oxygen supply which permits greater food intake and possibly because it decreases the cost of ventilation.

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Phosphorus and Iron Retention in Sediments Measured by Mass Budget Calculations and Directly

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CROSS, P. M., AND F. H. RIGLER. 1983. Phosphorus and iron retention in sediments measured by mass budget calculations and directly. Can. J. Fish. Aquat. Sci. 40: 1589 – 1597.

Retention of phosphorus (P) and iron (Fe) was estimated from mass budget calculations of Bob Lake, Ontario. Ratios of Fe to P in sediment cores were used to test the reliability of the concurrent retention estimated. However, a 300% range in Fe to P ratios measured in vertical profiles in sediments was many times larger than the uncertainty associated with mass budget measurements. Sediment cores showed a near-surface maximum of iron but not phosphorus. There was reasonably good agreement between P retention as computed by mass budget and by sediment accumulation methods, though the latter were slightly higher.

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La rétention du phosphore (P) et du fer (Fe) a été estimée à l'aide de calculs de bilan massique dans le lac Bob, en Ontario. Les rapports Fe:P observés dans des carottes de sédiments ont servi à vérifier la fiabilité de la rétention concurrente estimée. Cependant, une fourchette de 300 % dans ces rapports mesurés dans des profils verticaux de sédiments était de plusieurs fois supérieure à l'incertitude associée aux mesures de budget massique. Les carottes de sédiments montrent, presque à la surface, un maximum pour le fer mais non pour le phosphore. Il y a assez bon accord entre la rétention de P telle que déterminée par bilan massique ou par accumulation de sédiments, bien que cette dernière méthode donne des valeurs légèrement supérieures.

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THE annual retention of phosphorus in the sediments of a lake (R_P) has been shown to be a useful parameter in the prediction of mean summer chlorophyll *a* (Dillon and Rigler 1974) and hypolimnetic oxygen deficit (Cornett and Rigler 1980). It now appears that R_P can be predicted from the annual, areal water load to a lake (Kirchner and Dillon 1975; Ostrofsky 1978). However, the data from which the latter empirical relation has been derived are too few and the confidence limits of the prediction too broad. If empirical models involving R_P are to be tested and improved we will need both a larger data set and more confidence in the accuracy of R_P measurements. The latter can be achieved by developing alternative methods of measuring R_P as a check on the reliability of the mass balance method that estimates R_P as the difference between all measured inputs of P and output of P.

In the first comparison of two independently derived measurements of R_P, Evans and Rigler (1980a) compared the accumulation of P calculated from ^{210}Pb measurements of sediment accumulation and analyses of surface sediments for P, with R_P previously obtained by Cross (1977) from the mass balance method. Although the similarity between the two results was encouraging, further checks on the methods are essential. In particular, we need to know the extent to which any method involving analyses of sediments is biased by diagenesis of the substances under investigation.

Our first objective was to determine the retention of phosphorus and another element in a lake using mass balance measurements. The second was to investigate the retention of these elements in the sediments using sediment accumulation. Finally, the data used by Cross (1977) to calculate R_P in Bob Lake, the mass balance method, is made readily available.

The mass balance measurement of R_P was lower than that found by Evans and Rigler (1980a) by their method. To explain this discrepancy they suggested that P loading may have been underestimated, because cottage inputs were not included and measurement of aeolian loading of P is uncertain. A further potential difficulty in measuring P load arises from the sharp increase of phosphorus concentration that occurs in some types of headwater stream during flood runoff (Crisp 1966; McColl et al. 1975; Johnson et al. 1976). Rigler (1979) showed that if a routine sampling program involving weekly sampling were used to measure P export by such a stream, P loading from that stream would be underestimated by 27%. This error would cause the mass balance method to

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underestimate R_P because the lake inlets were all headwater streams.

Our rationale was that a more accurate mass balance estimate of retention might be made for an element other than phosphorus. The retention of this element and phosphorus could be compared with their retention calculated from sediment accumulation information. A discrepancy between the predicted and measured retentions would then indicate the magnitude of error in R_P.

We chose iron as the other element because it occurs in high concentration in Canadian Shield streams; it is efficiently retained in lakes (Schindler et al. 1976) and we suspected that its concentration in streams would fluctuate less than that of P. Also, preliminary measurements of Fe in bulk atmospheric fallout suggested that the aeolian input of Fe would be less important than that of P. Consequently, uncertainties in measurements of aeolian loading would be smaller when measuring R_{Fe} than R_P. Finally we chose iron because there was reason to believe that if phosphorus concentration were affected by diagenesis then Fe concentration might be correspondingly affected (Bloesch 1977; Bortleson and Lee 1974). This would facilitate corrections for effects of diagenesis if they were necessary.

Materials and Methods

Study Site and Hydrology

Bob Lake (44°54′N, 78°47′W), a 2.28-km^2 (not 0.23 as erroneously reported by Evans and Rigler 1980b) headwater lake, was previously used in P retention studies by Dillon and Rigler (1974) and in Pb and P accumulation studies by Evans and Rigler (1980a, b). Its 31.8-km^2 catchment is primarily mixed forest and swampy bushland. One inflow drains 61% of the catchment and 15 small streams drain 32%. The remaining 7% is drained by seepage or overland flow through no discernible stream channels and is referred to here as miscellaneous drainage area. We used the lake contour map constructed by Dillon (1974), but all areas were increased by 0.75% on the basis of remeasurement of the lake's surface area.

Outflow, storage changes, precipitation, and evaporation were determined on a daily basis from June, 1975 to June, 1976. We calculated inflow using the equation: Inflow = Outflow + Storage Change − Precipitation + Evaporation. As errors in the water budget will affect the elemental budgets, corroborating data were used as much as possible.

Discharge below the dam at the lake outflow was determined from a stage discharge rating curve. We used a Leupold Stevens Type F recorder with a 12.6-cm-diameter float to measure stage, and a Hydro-Bios dipping bar (Jens 1968) to measure discharge (Linsley et al. 1975). We used independent staff gauge readings at the dam to confirm outflow discharge (Cross 1977).

The water level of Bob Lake is controlled by a dam at the lake outflow. Spring runoff is stored for release throughout the summer, causing a lake level change of about 3 m in 1 yr. Changes in lake storage were calculated by multiplying change in lake level by lake area. Two Bristol depth-recording gauges, model 72-C-1186, equipped with diaphragm pressure systems, measured lake level continuously. Results were confirmed by regular visual measurements at each measuring site and independently at the dam.

We measured precipitation with a Kahlisco No. 31PM140 rain gauge on the shore of Bob Lake from mid-June to November, 1975 and mid-April to mid-June, 1976. When these data were available they were averaged with the daily precipitation data from the climatological station in Minden, 5 km away, to give daily precipitation. Results were also compared with precipitation collected weekly from two rafts on the lake. Snowfall measurements were taken by the Atmospheric Environment Service in Minden. Snowfall volume between December 21 and March 30 was accumulated and added directly into the lake between March 19, the first date of a prolonged period of above freezing temperatures in 1976 in Minden, and April 19, the date of the last ice on the lake for 1976. To estimate daily snow melt we calculated the daily outflow and storage change as a percentage of the total outflow and storage change over this time period and this daily percentage was applied to the total snowfall accumulation.

We obtained daily evaporation data from the nearest weather station at Lindsay Frost, 60 km away. The daily volume of water evaporated was calculated by multiplying depth of evaporation by lake surface area.

Because data for July 1975 were unavailable for the Lindsay Frost Station, average values from four surrounding stations were taken (Ottawa CDA, Kemptville, Hartington, and Toronto Met Res Station). These stations reported monthly values similar to those at Lindsay Frost on previous and subsequent montns.

No evaporation data were collected from October 30, 1975 to April 21, 1976. As the period from April to October accounts for 93% of the annual evaporation (Bruce and Weisman 1967), the measured lake evaporation was increased by 7% to give an annual evaporation.

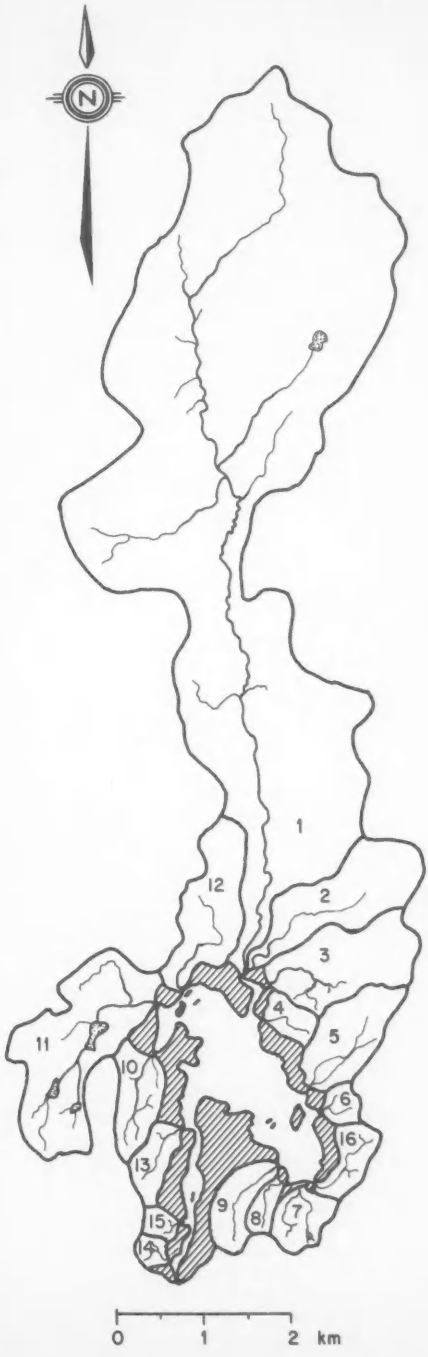
The catchment area drained by each stream was measured from 1:50 000 topographic maps (Fig. 1). Miscellaneous drainage areas were summed and treated as a single inflow. The calculated total daily inflow was apportioned to each stream and to miscellaneous drainage area by assuming a constant proportionality between runoff and catchment area.

Water Chemistry and Element Budgets

Water samples were collected by carefully dipping a 500-mL polyethylene bottle into the stream at a point where water flow was obvious and where bottom materials would not be resuspended by sampling. On site, 50-mL subsamples were immediately measured into 125-mL Erlenmeyer flasks in which they were subsequently digested for determination of total iron or phosphorus. Flasks were sealed with Parafilm until digestion.

Stream inflow No. 1, draining 61% of the total catchment, was sampled thrice weekly during spring and summer, whereas the 15 smaller streams were sampled weekly. All streams were sampled weekly in the autumn and biweekly in winter.

Rain rafts adapted from Gomolka (1975) were anchored on the lake to collect total wet and dry fallout (bulk precipitation). Two funnel collectors of differing diameter (9.8 cm



and 27.9 cm) were installed on each raft to ensure collection of an adequate sample during wet or dry weeks. Screens of 75-μm-mesh nitex were glued in the funnel to exclude large particles. Samples were collected weekly during the open water season using distilled water to wash down the funnels. Sample volumes were measured before subsamples were taken.

On February 26, 1976 a set of nine samples of the snow on the lake was taken. The melted snow volume was measured and subsamples were taken. Because old snow samples on the lake were taken, the measured concentration included dry fallout.

Dillon's (1974) modification of Strickland and Parson's (1972) method for total phosphorus analysis was used. This method uses perchloric acid digestion and colorimetric determination of a molybdenum blue reaction and is detailed in Dillon and Rigler (1974) Distilled water blanks and 10 $\mu g \cdot L^{-1}$ standards were measured with each set of samples.

The method for total iron analysis was a modification from American Public Health Association (1971) and Golterman (1969). The samples were digested with 5 mL of 9.5 $mol \cdot L^{-1}$ H_2SO_4 and evaporated until fuming had proceeded for 2–3 min. After cooling, 0.5 mL of 30% hydrogen peroxide solution was added, and the sample was reheated until the peroxide had evaporated. The samples were occasionally covered and stored overnight at this stage.

For the colorimetric determination of Fe, 10 mL of double-distilled water was added to each sample, and the pH of the solution was adjusted to pH 3.2–3.3 with 4 $mol \cdot L^{-1}$ NH_4OH. The final volume was adjusted to 50 mL with double-distilled water and 1 mL of 1.0% hydroxylamine solution and 1 mL of 0.5% *o*-phenanthroline solution were added. After the color reaction had proceeded for 3 h the samples were read in a Bausch and Lomb Spectronic 100 with a 1-cm path length at 508 nm. Double-distilled water blanks and 0.5 $mg \cdot L^{-1}$ iron standards were measured with each set of samples.

We calculated terrestrial loading for each stream separately by multiplying the measured element concentration on a given sampling date by the total discharge over the interval bracketing that date; these products were summed over the year. Input from miscellaneous drainage was not measured but was assumed to be equal to that from streams on a per unit area basis. Thus, miscellaneous drainage over any time interval was assigned 7% of the total terrestrial loading.

Aeolian loading was calculated from bulk precipitation data and analyses of accumulated snow. We calculated weekly loading from bulk precipitation as the product of the weekly volume of water collected by the raft's small funnels, plus washwater and the element concentration. The average winter accumulation of Fe and P per square metre of snow was calculated from analyses of cores of late winter snow. This accumulation was assumed to be melted into the lake between March 19 and April 19 at a rate proportional to water load. Output was calculated from measurements of P and Fe in outflowing water made according to the same sampling

FIG. 1. Catchment area of Bob Lake showing measured (numbered) and miscellaneous (shaded) drainage.

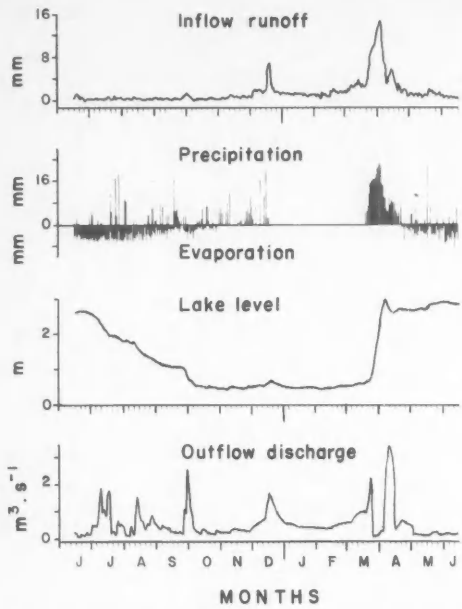


FIG. 2. Outflow discharge, lake level, precipitation, evaporation, and total inflow runoff for Bob Lake from June 16, 1975 to June 15, 1976.

regime used for Inflow No. 1. Fractional retention (R_P or R_{Fe}) was expressed as the fraction of the annual load of an element that remains in the sediments [(input−output)/input]. Annual retention is expressed as $mg \cdot m^{-2} \cdot yr^{-1}$.

SEDIMENTS

Fifty-one sediment cores were taken in a grid pattern from lake depths greater than 16.5 m with a K−B corer (Brinkhurst et al. 1969). The core tubes were stoppered and taken to shore where they were extruded and sectioned in 2-cm lengths within 4 h. Samples were stored frozen until freeze-dried. The dry sediment was powdered with a mortar and pestle. A 0.3-g sample was added to 50 mL of distilled water and analyzed by the same methods used for water.

As a check on the analytical method, 20 samples were analyzed in duplicate in our laboratory and at the Canada Centre for Inland Waters (CCIW). There was no significant difference in the results of P analysis, but our Fe results were 12.8% lower than those obtained at CCIW (Cross 1977). This difference remains unexplained but may result from differential digestion of iron. Analytical methods at CCIW used digestion with HNO_3 and atomic absorption technique. We assume that the CCIW analyses are correct and have applied a correction factor to all of our Fe results.

To calculate elemental retention from sedimentation data, we first calculated the regression of concentration of the element at the 14- to 16-cm slice in sediment on depth in the lake. This regression was combined with the regression of sediment accumulation rate on depth produced by Evans and Rigler (1980a) to calculate substance accumulation for each 5-m stratum of sediments. Their equation is

$$y = 2.95x + 25.17 \qquad (n = 13, r^2 = 0.97)$$

where y is sediment accumulation in $g \cdot m^{-2} \cdot yr^{-1}$ and x is sample depth in metres. Our value is equivalent to their minimum estimate as we have assumed that there is no accumulation of sediments at depths of less than 10 m.

Results

HYDROLOGY

Complete hydrological data are shown in Fig. 2. Lake stage, precipitation, evaporation, and outflow discharge are measured or extrapolated values: total inflow is calculated by difference to balance the water budget. The '0' reference level for lake level is the height of the dam with all stoplogs removed. Total precipitation during the study year was 971.4 mm which is 6.6% higher than the 20-yr average. Annual evaporation, taking into consideration the unmeasured period, was 751.7 mm. The measured outflow discharge and derived inflow discharge in Fig. 2 were calculated on a daily basis for calculation of iron and phosphorus budgets.

WATER CHEMISTRY AND BUDGETS

The behavior of Fe and P in the inflows was remarkably similar (Fig. 3). The concentration of both increased during June and July and decreased through August in Inflow No. 1. In early September and mid-October both elements showed similar short-term increases. From November to March the two had a slightly different pattern, with Fe showing a substantial increase in January−February. Phosphorus had lesser increases in late November and early February with a large peak late in March.

These differences did not obscure the strong relation between Fe and P which existed in all streams. Pooled data from Inflows 2−16 show a good linear correlation between Fe and P:

$$P = 0.0414Fe + 5.78 \qquad (n = 452, r^2 = 0.73)$$

where P and Fe are concentrations in $\mu g \cdot L^{-1}$.

The iron and phosphorus entering the lake are probably moving in the particulate phase, bound in a colloidal humic complex (Shapiro 1966). Any between-stream variability is probably obscured by the basic similarity of humic composition throughout the basin and the parallel response of iron and phosphorus to season and discharge.

The concentrations of both elements in the outflow remained fairly constant throughout the year. Iron values were about 80 $\mu g \cdot L^{-1}$ for most of the year but were higher from February to April with a peak of 330 $\mu g \cdot L^{-1}$ in March. The corresponding increase of Fe in the outflow, with a lag of about 1 mo, suggests that winter inflow does not completely

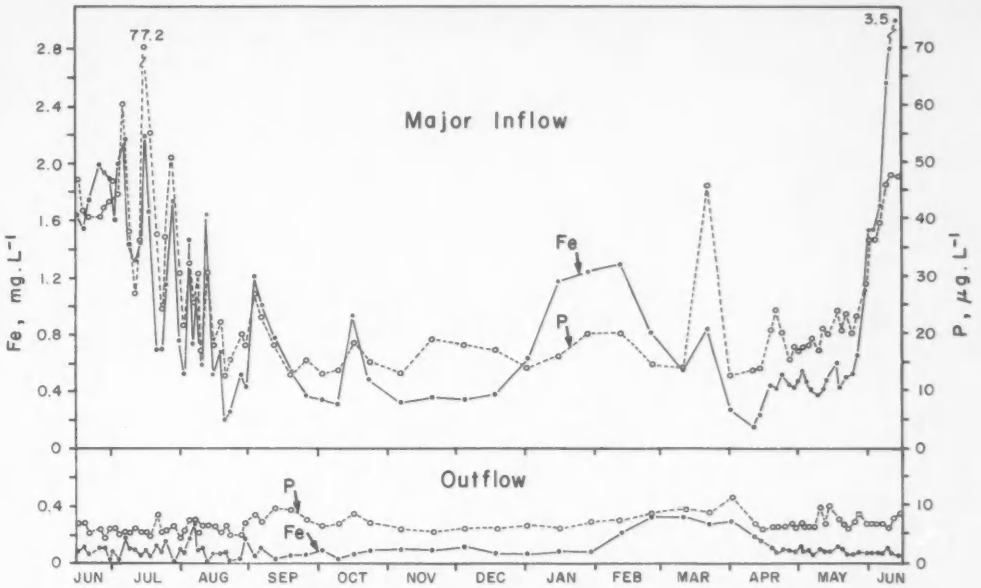


FIG. 3. Concentration of iron (Fe) and phosphorus (P) in the major inflow (Inflow No. 1) and the outflow streams of Bob Lake.

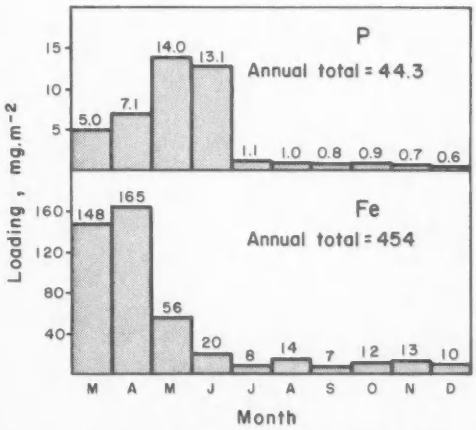


FIG. 4. Aeolian loading of Fe and P to the water of Bob Lake.

mix with the mass of lakewater. The concentration of P in the outflow was generally about 6 $\mu g \cdot L^{-1}$ in summer with a September peak of 9 $\mu g \cdot L^{-1}$ and a late March peak of 11 $\mu g \cdot L^{-1}$.

This evidence that meltwater P inputs do not mix completely into the lake metabolism has important implications for P-loading/productivity models. The use of P-loading for the full year may be inappropriate for northern lakes and the predictive relationship in these models might be improved if the P-loading in meltwater was excluded.

Aeolian input of Fe and P was highest in the spring (Fig. 4). No input was shown for January and February as the lake was frozen and snowfall was accumulated for input as meltwater. Because most aeolian Fe accumulated with snow and was delivered to the lake during spring melt, input was highest in March and April. Winter accumulation of P was also high but was dwarfed by inputs in May and June, presumably largely from pollen.

A monthly summary of the water, Fe, and P budget of Bob Lake is shown in Table 1. As expected the aeolian contribution (Fig. 4) of Fe was lower than that of P — 11% as opposed to 23%. In this respect the uncertainty of measuring input of Fe was indeed lower than that for P. Annual iron retention (76.6%) was not appreciably higher than retention of phosphorus (73.6%).

SEDIMENT ANALYSES

Vertical profiles of Fe and P for three cores taken from water 39–45 m deep are shown in Fig. 5. The concentration of iron slowly increases between 20 and 4–6 cm below the sediment surface, then increases rapidly to the surface. The thickness of this iron maximum is similar to that of the ^{210}Pb mixed layer (Evans 1980). The trend of P concentration was different from that of Fe and consistent with the results from three other Bob Lake cores previously reported by Evans and Rigler (1980a). There was no near-surface maximum of P. The Fe to P ratio in the sediments of Bob Lake changed from 15:1 at 18–20 cm below the surface to 45:1 at 0–2 cm, a 300% range in ratios.

TABLE 1. Monthly summary of water, iron, and phosphorus budget of Bob Lake, Ont., from June 15, 1975 to June 14, 1976. Adjusted retention takes into consideration the additional storage of Fe and P in the water column due to net lake storage change.

Period	Water load, mm	Lake storage, change %	Iron mg·m^{-2}		Phosphorus mg·m^{-2}	
			Total load	Output	Total load	Output
June 15–30	112	0.2	142	8	4.0	0.6
July	155	−4.1	214	71	8.5	4.5
August	117	−3.0	106	34	4.1	3.7
September	157	−2.1	96	35	3.6	3.9
October	142	−1.7	77	39	3.3	3.4
November	244	+0.1	108	32	5.3	1.9
December	962	+0.2	342	72	15.5	5.6
January	473	−0.2	395	39	8.0	3.4
February	490	+0.2	438	115	8.7	3.7
March	2194	+8.2	1238	284	57.7	8.6
April	1762	+3.0	610	232	31.9	9.3
May	468	+1.4	268	18	23.2	1.5
June 1–14	81	−0.3	175	6	17.5	0.5
Total	7357	+1.5	4209	985	191.3	50.6
Retention			3224		140.7	
Adjusted retention			3189		133.5	

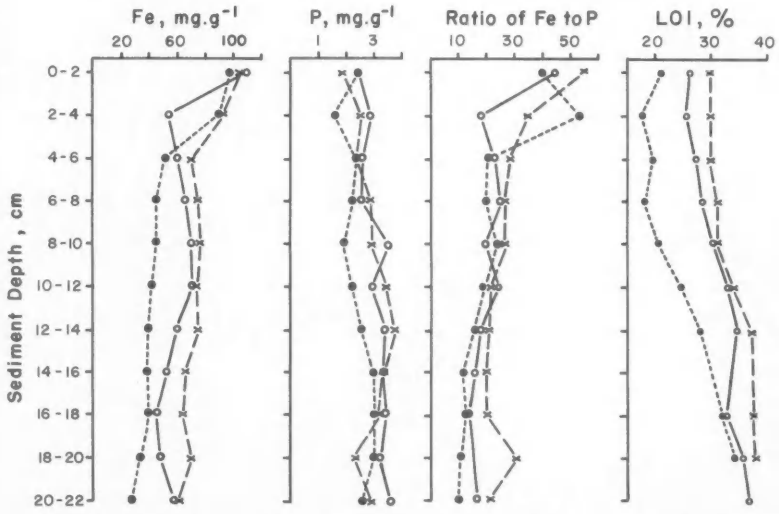


FIG. 5. Content of Fe and P in three sediment cores from Bob Lake. Cores were taken from 45 m (x), 43 m (○), and 39 m (●). Cores for LOI were taken from 47 m (x), 19 m (○), and 27 m (●).

Loss on ignition (LOI) was measured in a separate set of cores taken from water 19–47 m deep (Fig. 5) because these measurements were made after the material from the first cores had been used. Percent loss on ignition decreased continuously from 20 cm below the mud surface to the bottom of the mixed layer in all three cores.

As it was originally expected that deep sediments would be more representative of the chemistry of accumulating materials, most analyses were done on the 14- to 16-cm sediment slice. Data from Evans and Rigler (1980a) indicated that this sediment is about 300 yr old. For both Fe and P the concentration in this slice increased with water depth in the lake according to the equations:

$$\text{Fe} = 0.94d + 21.5 \qquad (n = 51,\ r^2 = 0.31)$$

and

$$\text{P} = 0.0202d + 2.08 \qquad (n = 49,\ r^2 = 0.20)$$

where elemental concentration is in mg·g^{-1} dry mass of

TABLE 2. Retention of phosphorus and iron in Bob Lake calculated from mass budget data and from ^{210}Pb measurement of sediment accumulation. All values are in $g \cdot m^{-2} \cdot yr^{-1}$ where total area is that of lake surface. Extrapolation gave an average 0–2 cm concentration of Fe 1.9 ± 0.39 times that at 14–16 cm.

Method	Sediment stratum analyzed, cm	Annual retention	
		P	Fe
Mass balance		0.134	3.19
Sediment accumulation	0–2	0.143	6.11
	14–16	0.173	3.22

sediment, and d is lake depth at sampling site in metres. We rejected two obviously anomalous values in our calculation of the phosphorus regression.

Depth alone explains only 31 and 20% of the variation between sites in iron and phosphorus content of sediments, respectively, and therefore a spatial pattern other than depth is more important. Because the data come from a spatial grid covering the whole lake, the retention of Fe and P has been more precisely measured than its variability as a function of whole water depth makes it seem.

The retention of P and Fe was calculated from sediment accumulation data and compared with values derived from mass balance (Table 2). The Fe concentration at stratum 0–2 cm used in calculating Fe retention from sediment accumulation was that obtained by ignoring the surface peak and extrapolating the gently increasing concentration from 20 to 4 cm to its intercept at zero depth. The agreement is reasonably good for both elements although the sediment accumulation method gives higher values than mass balance. At this stage, although the discrepancy is suggestive, it would be premature to speculate on its origin because there is a large uncertainty associated with the estimate of sediment accumulation (Evans and Rigler 1980a), and the mass balance estimate was derived from one year's measurements rather than long-term data.

Discussion

The need for an alternative mass budget method is more pressing than we at first realized. A simple comparison of our retention (73.6%) with that (72.5%) previously measured by Dillon (1974) is encouraging. However, the similarity is misleading: it was produced by three compensating differences. First, Dillon, who was simultaneously measuring retention in a large series of lakes, was unable to study the 14 small streams entering Bob Lake. For these he assumed a low phosphorus concentration equivalent to that measured in groundwater. Our measurements showed that the mean phosphorus concentration in these streams was similar to that in the main streams. Thus, our calculated terrestrial loading was 147 $mg \cdot m^{-2} \cdot yr^{-1}$ which was 83% higher than Dillon's. Second, Dillon determined the aeolian contribution of phosphorus from several land-based precipitation collectors located throughout his study area. Our measurements and those of Gomulka (1975) for the same region showed that aeolian phosphorus loading is lower when data are collected from lake-based sites. Thus, our calculated aeolian loading was 44 $mg \cdot m^{-2} \cdot yr^{-1}$ which was 42% lower than Dillon's. Third, Dillon based his phosphorus loss by the outflow on discharge calculated using dam data. As he pointed out (Dillon 1974), there are a number of errors associated with this method. Cross (1977) found that measured discharge was 31% higher than discharge calculated from dam data. Our measurements of lake output were 18% higher than Dillon's.

Other problems with the construction of input–output budgets are apparent. Input of phosphorus from shoreline cottages was not measured or estimated in either our study or Dillon's. Dillon and Rigler (1975) subsequently developed a method of including this component in estimates of P-loading.

Hydrological data form the basis of elemental budget models and a consideration of errors in estimates is important. Winter (1981) reviews the uncertainties associated with estimates of water balance in lakes. Our estimates of discharge using a stage discharge rating curve can be quite accurate (±5%, Winter 1981). Comparison of long-term records (Pentland 1968) agree with a mean error of 18% found by Scheider et al. (1978) for comparisons of this type (Cross 1977).

Daily precipitation estimates collected at the lake and in Minden were significantly different, probably because of the difference in collector design and frequency of collection as well as a result of the localized nature of thunder storms. Weekly precipitation, however, was comparable between these two sites and in comparison with data collected from the rafts on the lake.

No corroborating data were available for our estimates of evaporation but a large range of potential errors are discussed by Winter (1981). We excluded groundwater from our calculation because it was difficult to determine and would be negligible because of the impervious nature of the bedrock.

Our water balance for the lake was carefully measured with use of as much corroborating data as possible. The calculated inflow, however, includes any errors in measurements of the other components of the water budget. Obviously we must be cautious about using P retention from mass budget measurements as a standard against which other methods of measuring retention are compared. Small discrepancies (i.e. <25%) between results might equally well be due to errors in measurement of P-loading.

Concentrations of Fe and P in the sediments are independent despite the high correlation between the two affluents. The concentration of Fe in the surface-oxidized layer indicates that Fe diffuses upward from the reduced sediments and precipitates in the oxidized layer. Below the oxidized zone as P increases, Fe decreases. This is not a new phenomenon. In Ennerdale, an English lake morphometrically similar to Bob (cf. Macan 1970), the Fe to P ratio shows a trend similar to that in Bob Lake, but over most of the entire postglacial history of the lake (Mackereth 1966).

Our results show that it would be inappropriate to use surface concentration of Fe to calculate retention using sediment accumulation. This would grossly overestimate Fe retention. In the same way the use of deep sediment values of P concentration would increase the discrepancy between sediment-retention and mass-budget estimates of P retention.

It is apparent that study of Fe to P ratio in the sediments of Bob Lake might be useful in developing a simple theory

explaining the vertical changes in concentration of P and Fe. The decreasing concentration of phosphorus towards the sediment surface probably was caused by changing composition of sedimenting materials and not by downward migration of P. A possible cause of this slow change could be forestry operations and partial clearance of shoreline for cottages. These changes in the catchment of Bob Lake could have caused the phosphorus-rich organic sediments to be diluted with phosphorus-poor inorganic particles from the catchment. As there is no surficial rise of phosphorus concentration at the sediment/water interface, it appears that there is either no upward migration of P or that any migrating P escapes to the water. Consequently, we conclude that the P concentration in the surface sediment is the appropriate concentration to use in calculating P retention.

Iron differs from P in showing a slowly increasing concentration from 20 to 4 cm below the surface and an abrupt increase in the surface 2 to 4 cm. We postulated that the gentle gradient deeper in the sediments results from the same edaphic changes that influenced P concentration and that the sharp surface increase results from diagenesis of soluble iron that precipitates in the oxidizing conditions near the mud–water interface.

The results of the comparison of methods are consistent with the hypothesis we have presented to explain the concentration gradients of these elements in the sediments. As yet, little confirmatory evidence for the hypothesis is available. The purpose of the LOI analyses was to test the idea that the decreasing P concentration resulted from increasing dilution of P-rich organic sediments with inorganic particles. We found that the % ash increased towards the surface as predicted (i.e. the loss on ignition decreased). Further tests of this hypothesis are obviously needed, although one other observation is consistent with it. Evans (1980) noted that the decrease of unsupported ^{210}Pb with increasing depth in Bob Lake sediments was not always log-linear, but appeared to increase with increasing depth. This phenomenon could be caused by an increasing input of inorganic drainage basin materials in recent decades.

Acknowledgments

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Orientation of Chum Salmon (*Oncorhynchus keta*) After Internal and External Magnetic Field Alteration

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Groups of hatchery reared juvenile chum salmon (*Oncorhynchus keta*) from Conuma River, British Columbia, were tested for compass directional preferences in experimental tanks. Chum salmon generally moved in the direction appropriate for migration through Nootka Sound to the North Pacific Ocean. Fry orientation was not disrupted by covers over the tanks. Stainless steel coded wire tags inserted into the heads of the salmon had little effect, regardless of whether they were magnetized or not. A 90° change in the external magnetic field influenced fry directional movements, but the magnitude and direction of the change were not readily explainable.

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On a étudié dans des bassins expérimentaux les directions au compas préférées par des groupes de jeunes saumons keta (*Oncorhynchus keta*) élevés en pisciculture et provenant de la rivière Conuma, en Colombie-Britannique. En général, les saumonneaux se déplacent dans la direction appropriée à une migration par le détroit Nootka vers le Pacifique nord. Des couvercles placés sur les bassins ne dérangent pas l'orientation des alevins. Des fils métalliques codés en acier inoxydable insérés dans la tête des saumons n'ont que peu d'effet, que ces fils soient magnétisés ou non. Un changement de 90° du champ magnétique extérieur influence les mouvements directionnels des poissons, mais l'ampleur et la direction de ces mouvements s'expliquent difficilement.

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THE mechanisms guiding the migrations of Pacific salmon (*Oncorhynchus* spp.) have been the subject of considerable research. Although the upstream homing migrations of adults are guided principally by olfaction (Hasler et al. 1978), it has long been hypothesized that open water migrations are guided by other mechanisms (Hasler 1956). Experimental studies revealed that compass directional preferences facilitate the lake migrations of sockeye salmon (*O. nerka*) smolts (Groot 1965) and fry (Brannon 1972). These directional preferences are guided not only by celestial features such as the sun's position and light polarization patterns but also by the earth's magnetic field (Quinn 1980, 1982; Quinn and Brannon 1982). However, an attempt to determine the basis of magnetoreception in sockeye was inconclusive (Quinn et al. 1981).

To date, with the exception of Healey's (1967) pink salmon (*O. gorbuscha*) study, all research on juvenile salmon compass orientation has been conducted on sockeye. The goals of the present study were (1) to investigate the directional preferences of chum salmon (*O. keta*) fry about to migrate through an inlet to the open ocean to help determine the generality of compass orientation in juvenile salmon, and (2) to determine the relative roles of celestial and magnetic cues in directing the orientation of chum fry. In addition, the development of magnetized coded wire microtags as a tool for salmon management (Jefferts et al. 1963; Bergman 1968) provided an opportunity to (3) examine the possible influence on orientation of an internal magnetic field localized in the head of the fish.

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Methods

EXPERIMENTAL SUBJECTS

Adult chum salmon spawn in the fall, and fry emerge from gravel redds the following spring. Emergence occurs at night, and fry normally begin downstream movement to the ocean immediately (Neave 1966). After leaving estuaries, chum salmon generally move rapidly north, along the continental shelf of southeastern Alaska, before moving to offshore feeding areas (Hartt 1980). These migratory tendencies make chum salmon fry likely subjects for orientation experiments.

In early April, 1982, 60 000 chum salmon fry from the Conuma River Hatchery (Fig. 1) were allocated for orienta-

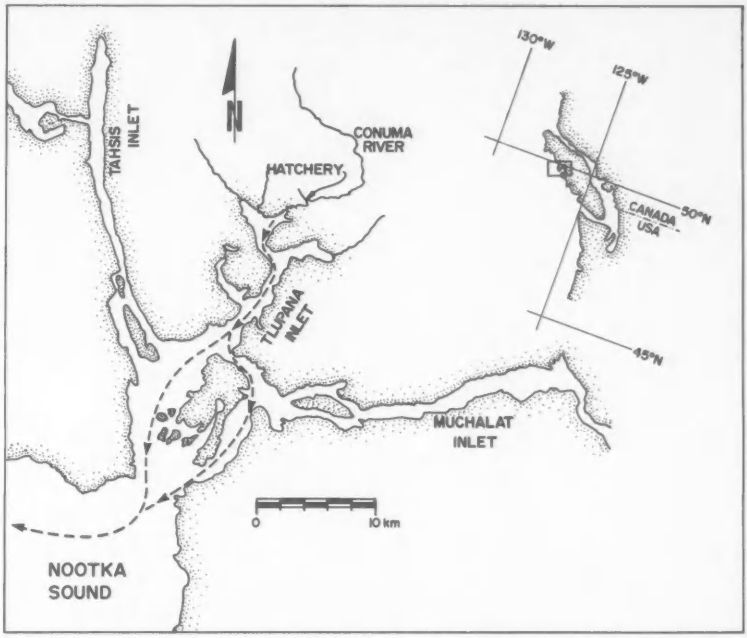


FIG. 1. Conuma River in relation to Tlupana Inlet, Nootka Sound, and Vancouver Island. Arrows indicate the general route of chum fry migration.

TABLE 1. Magnetic field measurements of magnetized and unmagnetized microtags. (A) Magnetizations measured with a Schonstedt SVM-1 susceptibility/viscosity magnetometer. (B) Measurements of the magnetic field from the tip of one of the magnetized tags, using a Bell 620 gaussmeter with a Hall effect probe.

A. Magnetic moment ($A \cdot m^2$)	
Magnetized tags	Unmagnetized tags
5.64×10^{-6}	1.56×10^{-7}
6.13×10^{-6}	0.35×10^{-7}
5.70×10^{-6}	1.88×10^{-7}
4.48×10^{-6}[a]	

B. Distance (mm)	Magnetic field (μT)
10	0.5
9	1.0
8	1.0
7	1.3
6	1.6
5	2.2
4	4.7
3	8.0
2.5	15.0
2	25.0
1.5	37.0
1	66.0

[a]Tag used for the measurements in (B).

tion tests. These fry, progeny of wild Conuma River fish, had hatched in early December and had been placed in outdoor feeding channels in late February and early March. During the experiment, the fry were held outdoors with an unobstructed view of the sky in six 1.8-m circular tanks with counterclockwise flowing water (2.7−4.5°C) and were fed daily. Fry averaged 51 mm fork length (SD = 3 mm) and 0.92 g (SD = 0.22 g) at the beginning of the experiment and grew to 54 ± 4 mm and 1.17 ± 0.29 g by the end.

TAGGING PROCEDURE

The operation of tagging salmon with coded wire microtags normally has two parts: tag insertion and tag magnetization. During tag insertion, a spool of stainless steel wire with coded data mechanically imprinted on it is advanced by rollers. A 1-mm segment of wire is cut and then pushed forward by the rest of the spool. The head of an anesthetized fish is placed in a mold and the 1-mm wire tag is inserted by the force of the wire behind it. X rays and dissection of tagged fry revealed the tags at or near the midline, above the upper jaw. At this location, a magnetized tag would generate an earth-strength field in much of the fry's head.

From April 6 to 10, chum fry were tagged with microtags. Each day, fry were sized and those under about 46 mm were rejected. The remainder were divided into three groups of 20 000. One group was tagged and the tags magnetized, the second group was tagged but the tags were not magnetized (to control for the effects of the tagging procedure), and the third group was handled similarly but was not tagged at all.

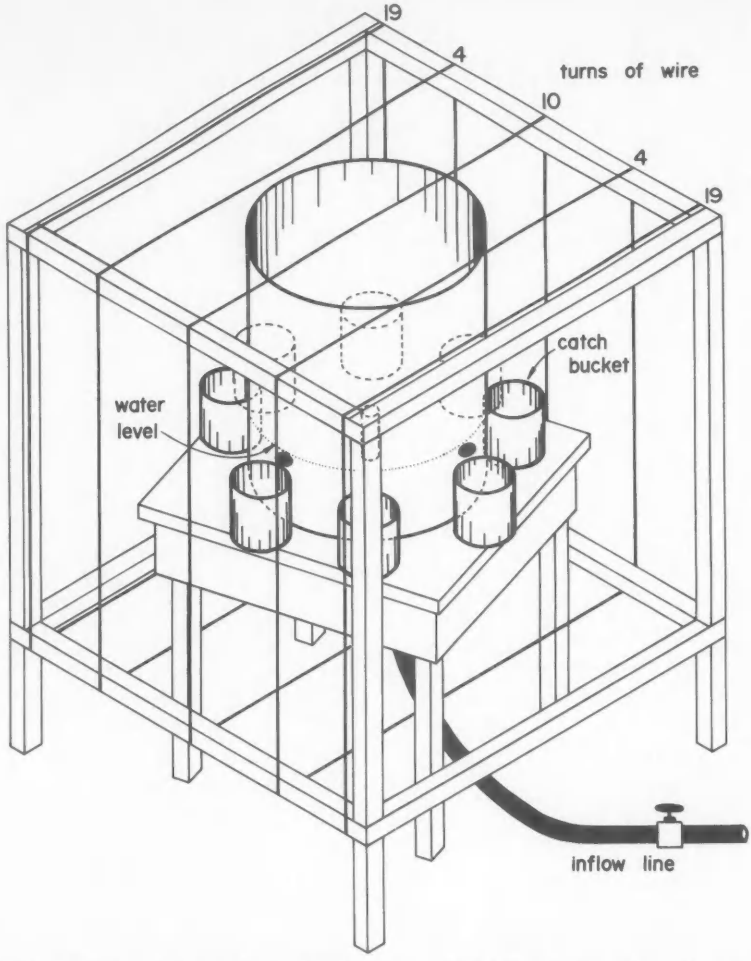


FIG. 2. Scale diagram of the cube coil used to alter the magnetic field (showing the numbers of turns of wire), and the testing tank. The tank is 61 cm wide and 66 cm deep; the surfaces of the cube are 122 cm.

The tags were magnetized by passing the fish through a 50-mT (500 gauss) circular magnet, ~1000× earth's field strength. This gave the tags a magnetic moment of $\sim 5.5 \times 10^{-6}$ A·m^2, roughly 40× the moment of tags that had not been magnetized (Table 1). After the tag was magnetized, the fish passed a metal detector, termed "quality control device (QCD)." In a small number of cases, the tag was inserted improperly and immediately fell out or was not inserted at all. Because 0.5% of the fish from the group with magnetized tags failed the initial QCD check, it is reasonable to assume that a similar proportion of the fish whose tags were not magnetized were in fact untagged.

After each day of testing, 200 fry with magnetized tags were checked for tag loss with the QCD. The rate of total tag loss rose from about 3% to roughly 10% at the end of the experiment. Early tag loss due to improper implantation is to be expected, and the tags that are not shed early are soon overgrown by the fish's skull. The 3–10% figures estimate the proportions of all tagged fish that had lost their tags by the time they were tested.

TESTING EQUIPMENT

Chum salmon fry were tested for directional preferences in 12 cylindrical polyethylene plastic tanks, filled to a depth of 12 cm with creek water drawn from above the hatchery (Fig. 2). Each tank received 52 L/min via a standpipe extending 16 cm from the bottom of the tank. Water flowed

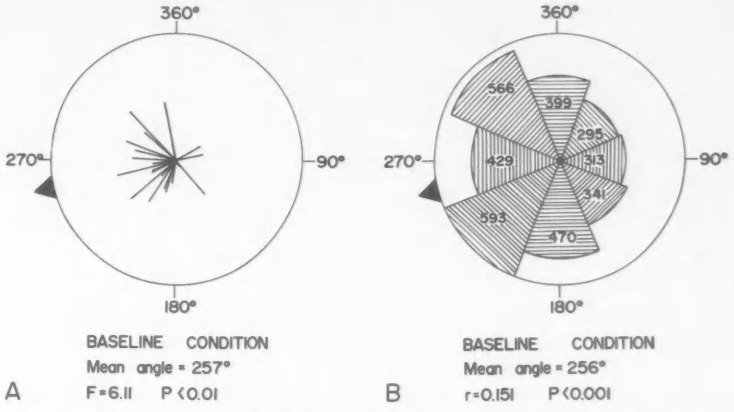


FIG. 3. Orientation of untagged chum salmon fry tested in the baseline condition (no cover, normal magnetic field). (A) Second-order analysis; each line depicts the mean bearing and concentration of one night's testing ($N = 20$). (B) First-order analysis; the numbers of fry trapped in the eight compass directions summed over 20 nights of testing.

to eight equidistant ports on the tank's perimeter. Fish swimming downstream (appropriate behavior for outmigration) were caught in buckets with overflow screens, after the design of Quinn and Brannon (1982).

The experimental design called for control over the availability of celestial and magnetic cues. Each night, six of the 12 tanks were uncovered, affording the fish a 40° view of the sky but not of the horizon or the other tanks. The remainder of the tanks had polyethylene covers which, like the tanks themselves, were translucent but permitted no image discrimination. To control the magnetic field, all tanks were centered in 122-cm cube coils (Rubens 1945). When connected to DC power supplies, these coils rotated the horizontal component of the earth's magnetic field 90° counterclockwise (putting north in the west) but did not affect either the total intensity or inclination of the field.

EXPERIMENTAL PROCEDURE

Six coils were turned on and the remainder were disconnected to serve as controls. The three groups of fish (untagged, tagged−not magnetized, and tagged−magnetized), the covers, and the activated coils were changed systematically on a daily basis so that all tanks were used to test all fish groups under all conditions. Tests were performed with all tanks for 20 nights from April 9 to 28.

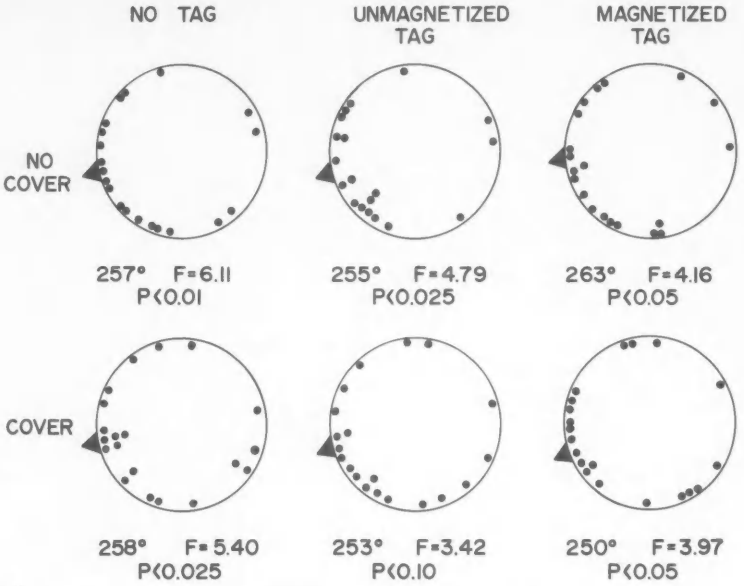
The testing procedure was as follows. About 30 min after sunset, 800 fry from each of the three groups were divided into four plastic pans for a total of 12 pans with 200 fish each. The fish were placed in the tanks without water flow. Six of the tanks were immediately covered, the magnetic coils for six having already been activated. After 5 min, the water was turned on, permitting volitional movement from the tanks in eight directions (magnetic N, NE, E, SE, S, SW, W, NW). At about 06:00 PST, before the sun's disk was visible over the horizon, the water was turned off, trapping the fish that had not moved in the center of the tank.

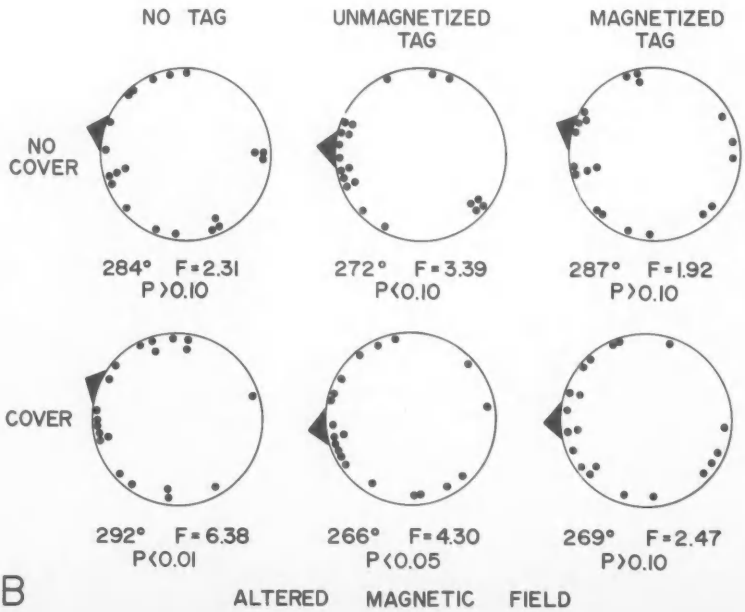
STATISTICAL ANALYSIS

The numbers of fish trapped in each direction and the number in the tank itself were tallied for each tank each morning. Mean bearings and statistical confidence levels were calculated for each test condition using the Rayleigh test (Batschelet 1965) on the raw data pooled over the 20 nights of testing. However, although counting individual fish reveals much about their movement patterns, this treats each datum point as independent, which they are not. Therefore, Hotelling's test was also used to determine the significance of the results, using each test release as a datum point, weighted for the concentration of fish bearings in that release

TABLE 2. Compass orientation of chum salmon fry in the normal and altered magnetic fields, comparing the results of tests conducted early and late in the experiment. Fish from all groups are pooled; covered and uncovered tests also combined. (*$P < 0.001$).

Magnetic field	Test nights	Sample size	Mean bearing	Rayleigh's r
Normal	4/9−19	11 627	241°	0.147*
	4/20−28	8 711	276°	0.142*
Altered (N→W)	4/9−19	11 591	278°	0.125*
	4/20−28	8 724	285°	0.111*


NO TAG
UNMAGNETIZED TAG
MAGNETIZED TAG
NO COVER
257° F=6.11 P<0.01
255° F=4.79 P<0.025
263° F=4.16 P<0.05
COVER
258° F=5.40 P<0.025
253° F=3.42 P<0.10
250° F=3.97 P<0.05
A
NORMAL MAGNETIC FIELD


NO TAG
UNMAGNETIZED TAG
MAGNETIZED TAG
NO COVER
284° F=2.31 P>0.10
272° F=3.39 P<0.10
287° F=1.92 P>0.10
COVER
292° F=6.38 P<0.01
266° F=4.30 P<0.05
269° F=2.47 P>0.10
B
ALTERED MAGNETIC FIELD

(Batschelet 1978). Comparisons among groups were made using the Watson−Williams test (Schmidt-Koenig 1975) for first-order data, and Hotelling's two-sample test for second-order data (Batschelet 1978).

Results and Discussion

Baseline Directional Preference

The orientation of untagged fish tested without covers in the normal magnetic field may be considered the baseline directional preference, against which the effects of covers, altered external magnetic field, or tags may be evaluated. Of the 4000 fish tested in the baseline condition, 3406 (85%) moved out of the tanks and into the catch buckets. Second-order analysis revealed a nonrandom distribution of test releases, with a mean bearing of 257° (Fig. 3A). Counting the fish individually yielded a 256° mean bearing (Fig. 3B). However, the distribution of individual fish was not completely normal, as the SW and NW exit ports were both preferred over the W port.

Chum fry migration out of Tlupana Inlet and Nootka Sound requires generally southwesterly movement (Fig. 1). This is followed by relatively rapid northwesterly movement up the coast of Vancouver Island, and north along the coasts of British Columbia and Alaska (Hartt 1980). Thus the westerly mean bearing of chum fry in the baseline condition (no tag, no cover, normal magnetic field) is geographically appropriate. The preference for both SW and NW over W is somewhat unusual, as a normal distribution was expected. The fry had been held in freshwater about 6−8 wk after emergence from the gravel, thus delaying their normal migration. Groot (1965) found that the migrations of sockeye salmon smolts out of a complex lake system were aided by compass directional preferences that changed with time, as appropriate for movement through the lake system. It is possible that some of the fry were displaying SW migratory orientation appropriate for Tlupana Inlet and other, presumably older, fry were displaying NW orientation up the coast of Vancouver Island. Fish tested in the normal magnetic field early in the season were oriented in a more southerly direction than those tested later (Table 2) but this may also be an artifact of the extended freshwater rearing period.

In any case, the generally westerly orientation would facilitate movement along the north side of Tlupana Inlet and Nootka Sound. It is reasonable to assume that temperature and salinity influence orientation behavior, and preference for saline water probably prevents the fry from ascending other inlets with tributaries to Nootka Sound (McInerney 1964). The presence of spontaneous directional preferences appropriate for migration in chum salmon fry is not unexpected, as sockeye and pink salmon also have directional preferences that facilitate the migrations of populations in particular systems (Groot 1965; Healey 1967; Brannon 1972; Quinn 1980; Brannon et al. 1981; Quinn and Brannon 1982). Studies of the actual movement patterns of sockeye smolts in Babine Lake indicated that they were well oriented (Groot and Wiley 1965; Groot 1972).

Effects of Covers and Altered External Magnetic Field

The orientation patterns of untagged chum fry tested with and without covers were virtually identical in the normal magnetic field (Fig. 4A). In the altered field, a northerly shift of some 25° was evident, relative to tests in the normal field (Fig. 4B). Analysis of the individual (first-order) data indicated that the bearings in the normal and altered field (uncovered and covered tests combined) were different ($F_{1,\infty} = 97.37$, $P < 0.001$). However, the more conservative Hotelling's two-sample test of second-order data detected no significant differences among any of the test groups of untagged fish. Besides the change to a more northerly bearing in the altered field, the only other effect was a slight reduction in concentration around the mean bearing when the fish in the altered field were permitted a view of the sky. However, the variance did not significantly differ from those in other test conditions (test by Watson and Williams, described by Emlen and Penney 1964).

The directional preferences of chum fry were also analyzed for within-season variation by dividing the testing period into early (4/9−4/19) and late (4/20−4/28) tests. (Because of inter-tank variation and the randomization schedule, an 11−9 division of test nights yields more representative averages than a 10−10 division.) Pooling covered and uncovered tests and all tag groups, the mean bearing of tests in the normal field changed from 241° to 276°, and the bearings in the altered field changed from 278° to 285° (Table 2).

In the normal magnetic field, covering the tanks had no effect on chum fry orientation. This is consistent with results of studies with sockeye fry (Quinn 1980). Sockeye smolts, on the other hand, often orient 180° away from the expected direction under covers (Groot 1965; Quinn and Brannon 1982). Because the "back azimuth" phenomenon is not well understood, it is not possible to state whether its absence in chum fry is significant or not.

When the magnetic field was rotated 90° counterclockwise, the chum salmon oriented roughly 25° clockwise of their bearing in the normal field (first-order analysis: 255°−281°, second-order analysis: 256°−279°). The difference between normal and altered field orientation was greater in earlier tests than in later ones, however. Based on sockeye studies (Quinn 1980), a 90° change in orientation in the altered field under covers would be expected, and the responses with a view of the sky might depend on cloud cover. Thus the change in orientation in the altered field was predicted, but its direction and magnitude were not. Although it is not possible to determine the reasons for the behavior of fry in the altered field, it is reasonable to assume that they entrained to some local cue during the days prior to testing. The directional

FIG. 4. Orientation of three groups of chum salmon fry (untagged, tagged with unmagnetized nose tags, and tagged with magnetized tags), tested with and without covers, in (A) the normal magnetic field, and (B) the altered magnetic field. The dots on the perimeters of the circles represent the second-order mean bearings of individual nights of testing ($N = 20$ in all cases).

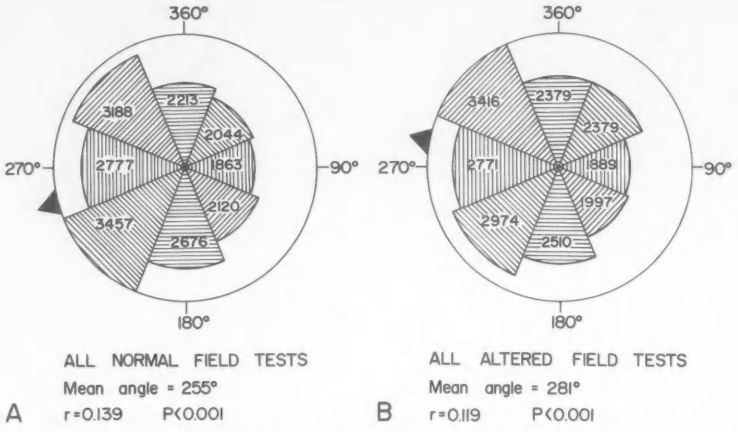


FIG. 5. Orientation of all chum salmon fry tested in (A) the normal magnetic field, and (B) the altered magnetic field, showing the numbers of fry trapped in the eight compass directions.

preferences displayed in the arenas were thus some combination of orientation to the magnetic field and to the entrained local cue.

THE INFLUENCE OF UNMAGNETIZED AND MAGNETIZED INTERNAL TAGS

Although handling and insertion of a 1-mm wire tag into the head of a salmon fry might seem to be a potentially lethal operation, the total mortality from April 7 to 28 was quite low in all three test groups: untagged = 131; tagged−not magnetized = 164; tagged−magnetized = 160. The directional preferences of tagged fish were similar to those of untagged fish (Fig. 4). The Watson−Williams test of first-order data indicated that all six test conditions in the normal field were statistically similar ($F_{5,\infty} = 1.14$), but it indicated variation in the altered field conditions ($F_{5,\infty} = 9.39$, $P < 0.001$). However, the pooled normal and altered field results were very different ($F_{11,\infty} = 147.91$, $P < 0.001$, Fig. 5). The more conservative two-sample second-order test indicated no differences within the normal and altered field groups. Although the pooled normal field data and altered field data differed from random (normal field: $F_{2,118} = 29.04$, $P < 0.001$; altered field: $F_{2,118} = 19.07$, $P < 0.001$), the 256° and 279° mean bearings were not significantly different ($F_{2,237} = 2.11$, $P > 0.10$).

Both first- and second-order analysis revealed weakest orientation in the altered field with a view of the sky. This pattern persisted in all groups of fish, but was most pronounced in the untagged fish (Fig. 4). In general, the concentration around the mean bearings was somewhat greater in tests with untagged fish, but the differences were very slight and not statistically significant.

Of the 20 nights of testing, eight had completely clear skies from evening release to morning termination, eight had completely overcast skies during these hours, and four had mixed cloud cover. The effect of cloud cover on orientation is best examined by considering tests in the altered magnetic field, as these present the fish with a conflict between sky cues and magnetic cues. In the altered field with no cover (all tag groups combined), orientation displayed under clear skies (274°, $r = 0.116$, $P < 0.001$) differed only slightly from that under overcast skies (288°, $r = 0.126$, $P < 0.001$).

The directional preferences of tagged fish were virtually identical with those of untagged fish. The slight decrease in concentration around the mean bearings for both groups of tagged fish was apparently a consequence of the tagging process itself. Considering the nature of the tagging process, it is perhaps surprising that the behavioral effects were so slight. As the fry apparently entrained to a local cue, the lack of effect of magnetized tags on compass orientation is difficult to interpret. Had the fish been forced to rely on the earth's magnetic field, the magnetized tag's influence on the magnetic field of much of the salmon's head might have affected orientation. However, the fish seem to be able to compensate for disturbance or loss of one sensory input by relying on others. Magnetic tags have been used routinely for years in coho and chinook salmon, with no substantial effect on homing success (Bergman 1968). These fish are tagged at a much larger size than the chum fry, however, and chum tagging has not been practiced long enough to have evidence of an effect on homing. Based on the present study, a substantial negative impact of tagging on chum salmon homing seems unlikely.

PATTERNS OF MIGRATORY ACTIVITY

On the average, 85% of the fish released into the tanks in the evening had left by morning, but the proportion was not constant. Although it did not vary according to external magnetic field, cover, or tag group, migratory activity varied from night to night (Fig. 6). There was no smooth pattern, but activity generally declined over the 20 nights of testing. Water temperatures increased only very slightly during this period,

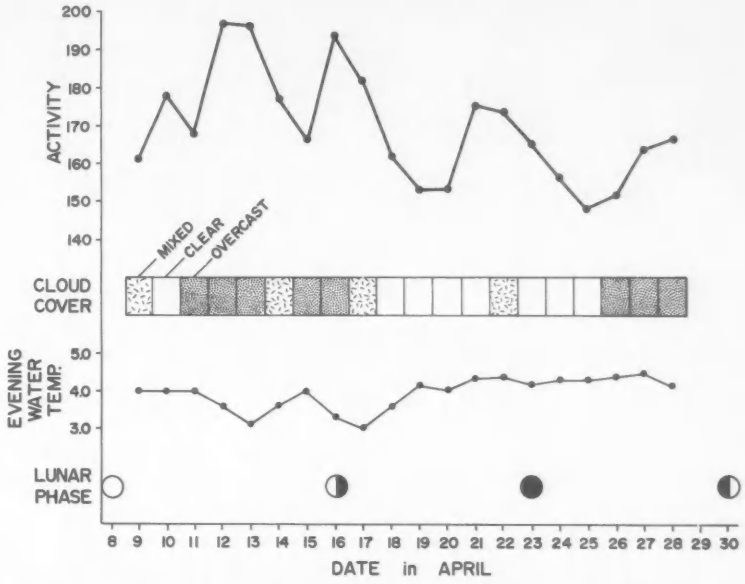


FIG. 6. The relationship between chum salmon fry migratory activity, represented by the average number of fry leaving the testing tanks each night (200 = total activity), and cloud cover, evening water temperature, and phase of the lunar cycle.

and the daily changes in activity did not seem to correspond to temperature fluctuations. The phases of the moon also had no clear relationship with fish movements. However, the cloud cover did correlate with activity. On clear nights, 80.7% of the fish left the tanks, and 87.6% left on totally overcast nights ($z = 18.62$, $P < 0.001$, difference of proportions test). On nights with mixed cloud cover, 86.8% of the fish left the tanks. Unfortunately, the present data set is not adequate to separate the effects of weather and date.

Acknowledgments

We owe a special debt of gratitude to Dr Peter Larkin, of the University of British Columbia, for his encouragement, advice, and support during the course of this study.

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Reproductive Cycles in Diaptomid Copepods: Effects of Temperature, Photocycle, and Species on Reproductive Potential

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WATRAS, C. J. 1983. Reproductive cycles in diaptomid copepods: effects of temperature, photocycle, and species on reproductive potential. Can. J. Fish. Aquat. Sci. 40: 1607 – 1613.

Periodic changes in the oviducts of *Diaptomus* characterize a reproductive cycle in which females oscillate between gravid and nongravid conditions. The duration of the nongravid condition sets an upper limit for rates of clutch production. In laboratory studies of *Diaptomus leptopus*, *D. pygmaeus*, *D. pallidus*, and *D. dorsalis*, the cycle was unaffected by photoperiod but showed a strong temperature dependency. At a given temperature, the four species had a common cycle period but spent different amounts of time in the two phases of the cycle. Interspecific differences in the duration of the nongravid phase produced substantial variation in reproductive potential.

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Des changements périodiques se produisant dans les oviducts de *Diaptomus* caractérisent un cycle reproducteur dans lequel les femelles oscillent entre des conditions gravides et non gravides. La durée de cette dernière condition fixe une limite supérieure au taux de production des portées. Au cours d'études en laboratoire avec *Diaptomus leptopus*, *D. pygmaeus*, *D. pallidus* et *D. dorsalis* on a constaté que le cycle n'était pas influencé par la photopériode, mais qu'il l'était fortement par la température. À une température donnée, les quatre espèces eurent un cycle de même période, mais montrèrent des différences dans la durée des deux phases du cycle. Comme résultat des différences interspécifiques dans la durée de la phase non gravide, il y eut substantielle variation du potentiel reproducteur.

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THE egg-ratio method allows one to describe the relative importance of the major demographic processes controlling population change in zooplankton (Edmondson 1960, 1968; Caswell 1972; Paloheimo 1974; Taylor and Slatkin 1981), but detailed mechanistic interpretations of field data often require additional biological information. In the case of birthrates, an understanding of reproductive physiology is needed to explain seasonal trends or to compare different populations. This paper deals with one aspect of copepod reproduction that may have a regulatory function in nature: a female reproductive cycle and its relation to potential rates of clutch production.

The reproductive rates of copepods that carry clutches of embryos in ovisacs depend on clutch size and the rate of clutch production. Both of these variables are potentially complex functions of environmental and physiological conditions. In the marine genus *Pseudocalanus*, however, both seem to depend primarily on temperature when food is abundant. Temperature operates through its effect on adult body-size to determine maximal clutch-size and through its effect on the duration of embryonic development to determine maximal rates of clutch production (McLaren 1963, 1965; McLaren et al. 1969; Corkett and McLaren 1969; Corkett and Zillioux 1975; Hart and McLaren 1978). Hypothetically, then, one may be able to estimate potential reproductive rates using only body-size and embryonic development time as predictors, both as functions of temperature.

Regulatory mechanisms are less clear in other calanoid genera. In the freshwater diaptomids, a positive correlation between body-size and clutch-size has been reported (e.g. Ravera and Tonolli 1956; Cole 1966; Smyly 1968; Maly 1973) but existing data do not explain the variation in body-size within a given species. We know little about factors affecting rates of clutch production. Eckstein (1964) showed that *E. gracilis* require remating before producing each clutch and that the interval between successive clutches was 25–50% longer than the developmental time of embryos. Robertson et al. (1974) reported similar data for *D. clavipes* showing, in addition, that temperature affected embryonic

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development and interclutch time (time without an ovisac) in different ways. Their data indicate that clutches were not produced as fast as they hatch (cf. *Pseudocalanus*), and that there is an optimal temperature for clutch production which is lower than the temperature at which embryos develop fastest. Possibly embryos develop much faster than gametes at some temperatures, as found in *Leptodora* by Kuzichkin (1975), but a simple explanation of these data is precluded by the remating requirement in *Diaptomus* (behavioral effects cannot be discounted) and because existing information on oogenesis in calanoid copepods is generally limited to histology and morphology (e.g. Ishikawa 1891; Hilton 1931; Lowe 1935; Marshall and Orr 1955; Conover 1967; Razouls 1974, 1975).

In a recent study, observation of *D. leptopus* showed that reproductive potential, in terms of clutch production, could be predicted from gross aspects of the female gametogenic cycle (Watras and Haney 1980). Females oscillated between gravid and nongravid reproductive conditions (distinct from ovigerous/nonovigerous conditions which refer to the presence of an ovisac) and the oscillations were observable in live, free-swimming adults. The characteristics of this cycle were defined at 18°C (L:D 8:16) under food replete conditions, and the duration of the nongravid phase was shown to represent the minimal interval between successive clutches. Under these conditions, females were physiologically capable of producing another clutch as soon as the one being carried was dropped.

My objectives here are to show how the oviducal cycle differs between diaptomid species, how it is affected by temperature and photocycle, and what effect these factors have on reproductive potential.

Methods

Immature copepodids (CI–CII) were collected in the field, individually isolated in 30-mL vials of filtered pond water (Whatman GF/C) and reared to maturity under experimental conditions. Mixed green algae, *Westella*, *Scenedesmus*, *Ankistrodesmus*, and *Chlorella*, were added 3 times per week to maintain food levels around 5×10^4 cells·mL^{-1}. Culture medium was replaced weekly and sediment was removed by pipet. The vials were kept in environmental chambers with illumination from 7.5- or 10-W incandescent lamps ($\sim 8 \times 10^{-5}$ W·cm^{-2}). Survival to maturity varied from 80 to 100%.

The species cultured were (1) *D. leptopus* from a shallow farm pond (area, 2500 m^2; maximum depth, 2 m) in Madbury, NH; (2) *D. pygmaeus* from Stonehouse Pond, a relatively large, mesotrophic lake (area, 60 000 m^2; maximum depth, 17 m), in Barrington, NH; (3) *D. pallidus* from a pond near Durham, NC; and (4) *D. dorsalis* from a reservoir near Miami, FL. *Diaptomus leptopus* were cultured at 12, 15, 18, 21, 24, and 27°C (± 0.5°C) with up to four photocycles at each temperature (LD 8:16, 12:12, 16:8, and 24:0). *Diaptomus pygmaeus* were cultured at 12, 18, and 24°C (± 0.5°C) with two photocycles at each temperature (LD 8:16 and 16:8). *Diaptomus pallidus* and *D. dorsalis* were cultured at 23°C (± 1°C) with one photocycle (LD 12:12).

Female *D. leptopus* and *D. pygmaeus* maintained at 12, 18, 21, or 24°C were also cultured together with males (two males per female) to estimate the duration of embryonic development and the rate of clutch production under laboratory conditions.

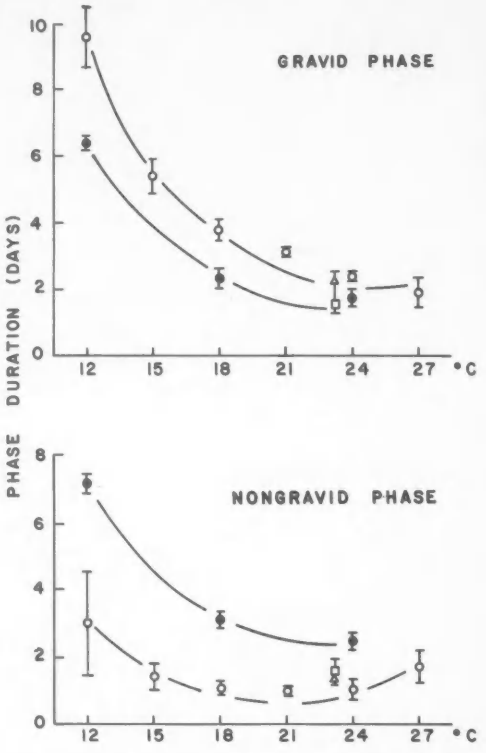

FIG. 1. Effect of temperature on the gravid and nongravid phases of the oviducal cycle in *Diaptomus* (data are means ±95% CI; ○ = *D. leptopus*, ● = *D. pygmaeus*; □ = *D. pallidus*, and △ = *D. dorsalis*.

After maturing, females were observed with a dissecting microscope (10×, transmitted light and red filter at night) at intervals of 8 or 12 h. The copepods were not removed from their vials or otherwise disturbed during inspection. When a change was noted (i.e. gravid to nongravid, ovigerous to nonovigerous), the point midway from the previous observation was designated as the time of occurrence. Each individual was observed through three or more changes in reproductive condition.

Results

All the females observed oscillated between gravid and nongravid conditions. The cycles were unaffected by photoperiod but showed a strong temperature dependency. At a given temperature, all species cycled at roughly the same frequency but the proportion of the cycle spent in each phase varied between species. When the duration of the nongravid

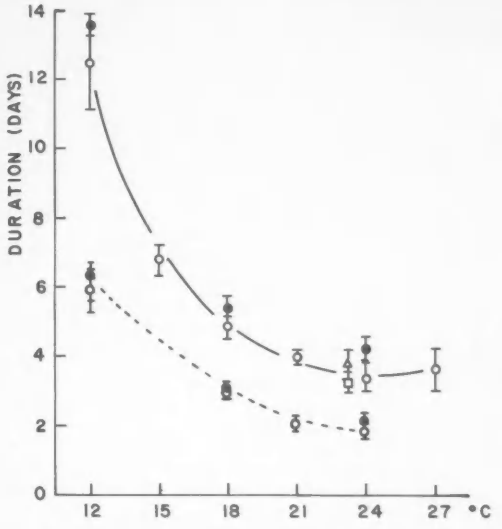

FIG. 2. Effect of temperature on the period of the oviducal cycle (solid line) and on the duration of embryonic development (broken line) in *Diaptomus* (symbols as in Fig. 1).

phase was compared to the duration of embryonic development, this interspecific variation implied a substantial difference in reproductive potential.

Photocycle had a negligible effect on the duration of either phase of the oviducal cycle of *D. leptopus* or *D. pygmaeus*. Analysis of variance did not show statistically significant differences ($P < 0.05$) due to photocycle. Phase-onset also appeared to be independent of the light regime. At least, there was no tendency for the nongravid phase, which has the most clearly defined onset of the two phases, to begin during any particular observation interval. (At the onset of the nongravid phase, ova are shed through the genital opening, a process completed in minutes. New gametes then move into the oviducts and gradually mature as the gravid phase onsets.) Thus, although the observation intervals were rather widely spaced for firm conclusions about onset timing, the data indicate that female *Diaptomus* cycle independently of the photocycle.

In contrast, the effect of temperature was relatively strong (Fig. 1). The duration of the gravid phase decreased with increasing temperature in both *D. leptopus* and *D. pygmaeus*. In *D. leptopus*, the nongravid phase appeared to reach a minimum around 21°C; beyond this temperature, the phase length increased, implying that temperatures near 21°C were optimal for gamete maturation. With *D. pygmaeus*, there were not enough data to determine accurately the functional response to temperature but, as a first approximation, both *D. leptopus* and *D. pygmaeus* seemed to show the same general type of temperature dependency.

Although the effects of temperature and photocycle were not examined with *D. pallidus* or *D. dorsalis*, oviducal cycles were evident in both species and the phase durations were within the range observed with *D. leptopus* and *D. pygmaeus*. This indicated that the oviducal cycle may be characteristic of the genus and generally useful, perhaps, in estimating maximal rates of clutch production.

When the data for all the species were plotted together, they strongly suggested that a single equation could be used to predict the period of the oviducal cycle from temperature (Fig. 2). Additional observations are needed to confirm this, but regression analysis of the available data indicated that the function:

$$\log P = 10.03 - 13.31(\log T) + 4.86(\log T)^2$$

where P is the cycle period in days and T is temperature in °C, describes the existing data well ($R = 0.94$, SD = 0.07, $n = 142$). All four species, then, appear to be cycling at the same frequency. The allocation of time to the gravid and nongravid phases differs between species, however (Fig. 1). *Diaptomus leptopus* are nongravid only about 25% of the time whereas *D. pygmaeus* spend about 60% of the cycle in the nongravid phase. These percentages remain fairly constant at all temperatures. *Diaptomus pallidus* and *D. dorsalis* are intermediate between these extremes, spending about 50 and 40% of their cycles, respectively, in the nongravid condition. Because a short nongravid phase implies potentially rapid clutch turnover, these interspecific differences could have a significant impact on rates of clutch production depending on the corresponding rates of embryonic development.

The relationship between temperature and embryonic development for *D. leptopus* and *D. pygmaeus* is described well by a negative power function (Fig. 2). Although statistically distinguishable, actual differences between species are small within this temperature range. A more striking difference is seen when the nongravid phase durations are plotted relative to the duration of embryonic development (Fig. 3). At all temperatures, *D. pygmaeus*' nongravid phase is longer than or approximately equal to the duration of embryonic development. Because fertilizable ova are not available until the end of the nongravid phase, this means that *D. pygmaeus* should not be able to produce a new clutch until sometime after a previous clutch hatches. One would expect, then, a physiologically required interclutch period which changes with temperature. With *D. leptopus*, on the other hand, the nongravid phase is usually shorter than the time needed for embryonic development. Females are generally ready to remate well before a clutch hatches. As a result, potential rates of clutch production are higher because there is no physiological constraint (other than the remating requirement) resulting in a mandatory time period between clutches.

Maximal rates of clutch production were predicted for these two species using both the nongravid phase duration and a common estimate of embryonic development (Fig. 4). Rates measured under laboratory conditions are also plotted with the predicted curves. The tentative conclusion is that *D. leptopus* can produce clutches at a much faster rate than *D. pygmaeus* under certain conditions (i.e. more than 3× faster at 16°C), and that maximal production rates for both species follow the trends in nongravid phase duration rather than the duration of the egg stage. With *D. leptopus* maximal rates are generally higher than rates of embryonic development and with *D. pygmaeus*, lower. Average turnover rates for both species

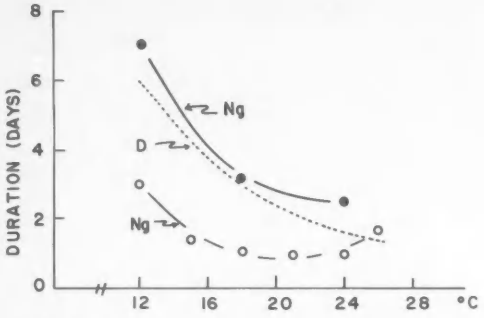

FIG. 3. Comparison of functions describing the nongravid phase (Ng) in *D. pygmaeus* (●—●) and *D. leptopus* (○—○) with a common estimate of embryonic development time, *D* (---). Note that for *D. pygmaeus*, Ng ≥ *D* whereas for *D. leptopus* Ng < *D*. All curves derived by regression techniques.

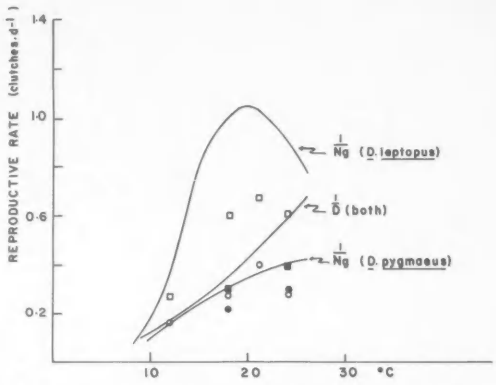

FIG. 4. Comparison of observed and predicted rates of clutch production for *D. leptopus* and *D. pygmaeus*. Predicted rates based on the nongravid phase (1/Ng) for each species or a common estimate of embryonic development time (1/*D*), all shown as solid lines. Points indicate observed rates (*D. leptopus*: □ = maximum observed rate, ■ = average observed rate; *D. pygmaeus*: ○ = maximum rate, ● = average rate).

are similar and low, and in both cases they are poor estimates of reproductive potential.

Implicit in these conclusions about the relationship between reproductive potential and the oviducal cycle is the assumption that the duration of the nongravid phase does not change when females are mated. Data for *D. leptopus* and *D. pygmaeus* indicate that this assumption is valid; when estimated at 18 and 24°C, the average nongravid phase of mating and isolated females was the same.

Discussion

The reproductive cycles of *D. leptopus* and *D. pygmaeus* are compared diagramatically on Fig. 5. In *D. pygmaeus*, the duration of the nongravid phase is generally longer than the duration of embryonic development. Gamete maturation is timed so that a female is able to remate soon after a clutch hatches, but not before. In contrast, *D. leptopus* are able to remate much earlier. But, since subitaneous clutches are generally carried until hatching and take the same time to develop in both species, the advantage of a short nongravid phase is not immediately apparent. At least two explanations seem tenable, both dealing with habitat.

First, differences in life cycle and habitat probably cause *D. leptopus* to be more dependent on the ability to produce resting eggs rapidly. *Diaptomus leptopus* are large (prosome lengths were 0.95−1.70 mm in weekly samples taken over 2 yr, $n = 800$) and typically inhabit shallow lakes or small ponds with no planktivorous fish (Cole 1961; Hazelwood and Parker 1961; Patalas 1964; Sawchyn and Hammer 1968; Winner 1970; O'Brien et al. 1973). Our specimens were taken from a pond which often dries to a depth of 10 cm or less in late summer and freezes to the bottom in winter. They overwinter as benthic resting eggs which hatch in the spring when water temperatures reach 10−15°C. Because resting clutches are carried for less time than subitaneous clutches (Watras 1980), shortening the nongravid phase is one way to facilitate their production. Second, predator avoidance may prove to be more important for *D. pygmaeus* than the enhancement of reproductive potential afforded by a short nongravid phase. This species is smaller (prosome lengths were 0.7−0.9 mm in monthly samples taken over 1 yr, $n = 260$) and typically inhabits deeper lakes with less dramatic seasonal variability. In Stonehouse Pond they are normally abundant in the water column all year and, although they do produce resting eggs, the diapausing clutches seem to remain attached to females for the winter. Because size, shape, and pigmentation all seem to affect the likelihood of being eaten by fish (e.g. Brooks and Dodson 1965; Zaret 1972; Zaret and Kerfoot 1975; Vinyard and O'Brien 1975; O'Brien et al. 1976), and, because major shifts in pigmentation occur during the oviducal cycle, a long nongravid phase might make this copepod less conspicuous and, therefore, less vulnerable to predation.

The ratio of egg stage to nongravid phase duration may, along with the differences in clutch size observed by Cole (1966), distinguish diaptomid species from permanent and impermanent environments. High ratios indicate high potential clutch production and, particularly if the clutches are larger, a marked enhancement of reproductive potential. (The range of clutch size for *D. pygmaeus* and *D. leptopus* in the study ponds was 3−22 and 8−100 eggs, respectively.) This hypothesis assumes, among other things, that the duration of the egg stage is relatively constant within the genus. Although statistically significant differences can be demonstrated between species (and within species as a function of parental temperature history, Cooley and Minns 1978), Bottrell et al. (1976) have shown that the duration of embryonic development is remarkably conservative in *Diaptomus* over a wide range of temperature.

Since the duration of the nongravid phase was not related to photocycle or to the latitude from which specimens were collected, seasonal trends in potential rates of clutch production are more likely driven by temperature than daylength. However, with species like *D. leptopus*, daylength may affect rates of clutch production indirectly through diapause

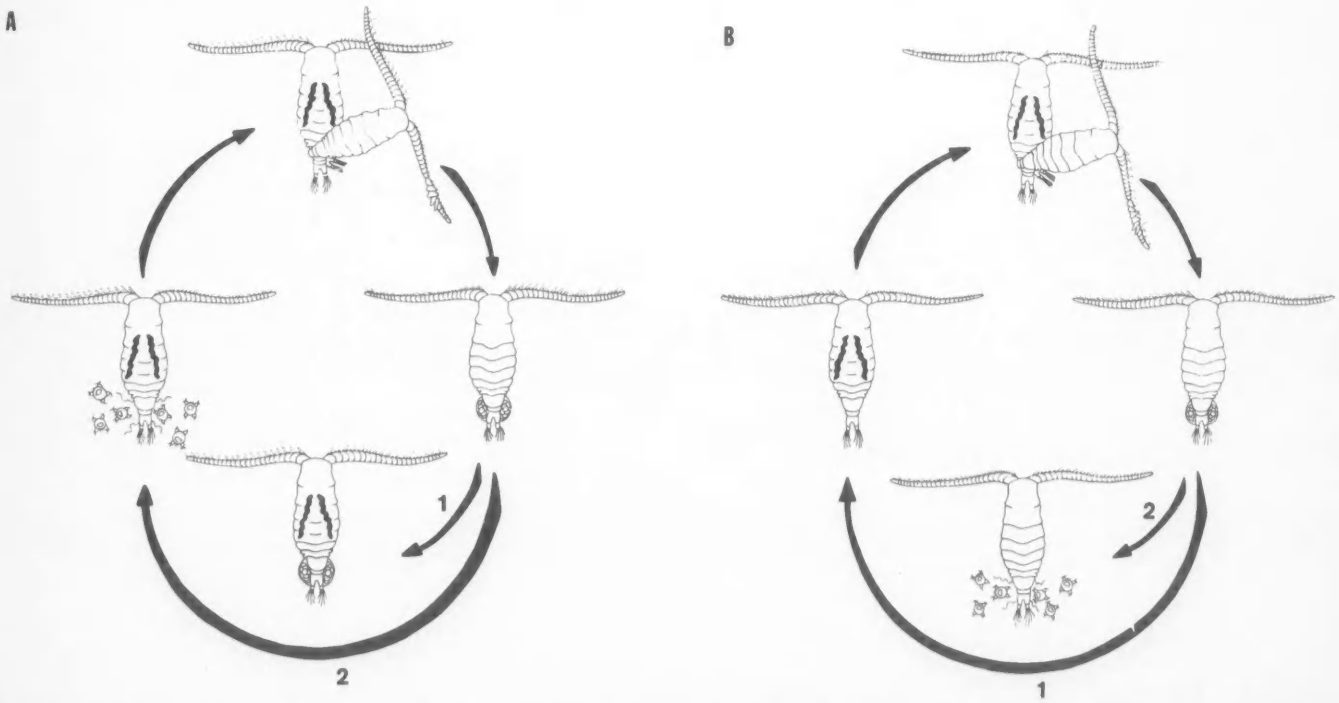

FIG. 5. Comparison of reproductive cycles in *D. leptopus* (A) and *D. pygmaeus* (B). Arrows 1 and 2 indicate relative amount of time needed for gamete maturation (i.e. nongravid phase) and embryonic development, respectively, in each case. In case A, gametes mature before embryos and the female is physiologically ready to remate before the eggs hatch (i.e. if the clutch is dislodged prematurely or if it is a resting clutch). In case B, the female cannot remate until some time after hatching.

induction. Photocycle-dependent diapause induction may be common among arthropods, especially insects, and has been reported for crustacean zooplankton (e.g. Grice and Marcus 1981; Marcus 1982). Since resting clutches are carried for less time than subitaneous eggs, a shift in the type of egg produced would also mean a change in potential rates of clutch production. Under such a mechanism, one might expect latitudinal effects to appear as differences in the ability to shift production from one egg type to the other in response to photocycle.

To summarize, the oviducal cycle described initially with *D. leptopus* (Watras and Haney 1980) is apparently common in diaptomid copepods and hence the characteristics of the cycle can be useful in predicting or comparing reproductive potential and regulatory mechanisms which affect copepod populations. Factors affecting phase durations can influence potential rates of clutch production in a predictable way and interspecific differences in cycle phasing can produce substantial variation in reproductive potential. This variation may, in turn, represent adaptation to particular habitats.

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"Colloidal" Phosphorus Errors in Gel Chromatography

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BURNISON, B. K. 1983. "Colloidal" phosphorus errors in gel chromatography. Can. J. Fish. Aquat. Sci. 40: 1614 – 1621.

Gel chromatography has been used for the separation of $^{32}PO_4$ and a high molecular weight "colloidal" ^{32}P-labeled fraction from $^{32}PO_4$-labeled lakewater. When the labeled filtrate is treated with reagents required for the molybdenum blue method for orthophosphate analysis, only a small fraction of the "colloidal" peak is hydrolyzed to orthophosphate. As the reduced molybdophosphoric acid is strongly adsorbed to the dextran gel, quantitative elution of $^{32}PO_4$ can be achieved with 0.05 mol·L^{-1} NaOH and 0.3% NaCl. In hardwater lakes, care must be taken to eliminate the possibility of orthophosphate precipitation at higher pH. In these lakes, it is unlikely that the discrepancy between $^{32}PO_4$ bioassays and chemical analyses can be solely attributed to acid hydrolysis of "colloidal" phosphorus. Microparticulate apatite also has the potential to release soluble reactive phosphate when the acidic molybdenum blue method is used.

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La chromatographie sur gel a été utilisée pour séparer le $^{32}PO_4$ d'une fraction « colloïdale » de poids moléculaire élevé marquée au ^{32}P dans de l'eau de lac marquée au $^{32}PO_4$. Quand le filtrat marqué est traité avec les réactifs nécessaires pour le dosage de l'orthophosphate par la méthode du bleu de molybdène, seulement une petite fraction du pic « colloïdal » est hydrolysée en orthophosphate. Puisque l'acide molybdophosphorique réduit est fortement adsorbé au gel de dextrane, il y a élution quantitative de $^{32}PO_4$ avec 0,05 mol·L^{-1} de NaOH et 0,3 % de NaCl. Dans les lacs d'eau dure, on devra éliminer la possibilité de la précipitation d'orthophosphate à des pH plus élevés. Dans de tels lacs, il est peu probable que la différence entre les analyses biologiques avec $^{32}PO_4$ et les analyses chimiques soient attribuables à la seule hydrolyse acide du phosphore « colloïdal ». L'apatite microparticulaire peut également mettre en liberté des phosphates réactifs solubles quand on utilise la méthode du bleu de molybdène acide.

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GEL chromatography has been used over the past decade to separate the ^{32}P-labeled fractions from lake water spiked with radioactive orthophosphate ($^{32}PO_4$) (Lean 1973 a, b, c; Lean and Nalewajko 1976; Paerl and Lean 1976; Downes and Paerl 1978; Paerl and Downes 1978; Peters 1978; White and Payne 1980). The gel most commonly used has been Pharmacia's Sephadex G-25 (medium). The three major radioactive peaks found in the lakewater filtrate, using a 0.45-μm filter, have been termed: colloidal phosphorus (void volume peak), XP (small molecular weight compounds), and orthophosphate (Lean 1973 a, b, c). The colloidal phosphorus peak is really a pool of various materials present in lake water ranging in size from less than 0.45 μm (particles) to truly dissolved compounds with molecular weights exceeding the exclusion limit of Sephadex G-25, or 5000 daltons. Therefore, although this peak will undoubtedly contain some colloidal material, subsequent reference to this fraction will be by the term "colloidal" phosphorus peak.

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Rigler (1966, 1968) suggested that the molybdenum blue methodologies overestimate dissolved orthophosphate concentrations by 10–100 times, and this is most likely caused by interfering elements and/or organic phosphorus compounds hydrolyzed by the acidic reagents. Rigler (1966) came to this conclusion based on the inconsistencies between a radiobioassay he developed (which gives a maximum concentration for bioavailable phosphorus) and the soluble reactive phosphorus (SRP). Rigler's observations have been substantiated by various researchers (Peters 1978; Levine and Schindler 1980; Tarapchak and Rubitschun 1981). The search for the cause of this inconsistency has continued to the present time. Chamberlain and Shapiro (1973) and Tarapchak et al. (1982) showed that particles <0.45 μm and >0.1 μm may be the source for SRP overestimation of orthophosphate. The composition (organic or inorganic) was only speculative. Downes and Paerl (1978) reported significant concentrations of a high molecular weight phosphorus component (RHMW-P) from Whatman GF/C lakewater filtrates, eluting at the void volume of a Sephadex G-25 column, which reacted

with their molybdenum blue reagent. The RHMW-P was also reported to be eventually used by P-starved *Chlorella* cultures (Paerl and Downes 1978). White and Payne (1980) did a more extensive study, on the lakes and streams of the central volcanic plateau of the North Island, New Zealand, and found that high concentrations of RHMW-P were mainly present in eutrophic lakes and that only 24–88% of the RHMW-P was used by the *Chlorella* depending on the lake. The conclusion reached was that the interpretation of dissolved reactive phosphorus in terms of bioavailability is probably impossible whenever RHMW-P is present (White and Payne 1980). In addition, White et al. (1981) demonstrated that the near-surface waters of 32 lakes, including some studied by Rigler (1964), did not contain sufficient RHMW-P to be a major influence causing discrepant estimates of orthophosphate (as measured by molybdenum methodologies) and radiobioassays. White et al. (1981) speculated that perhaps the low molecular weight phosphorus compounds are reactive and cause the overestimation of orthophosphate. Chamberlain and Shapiro (1973) suggested that molybdate procedures using normal temperatures and short acid exposure times (Chamberlain and Shapiro 1969) would greatly reduce the significance of any error introduced by the hydrolysis of organic phosphate esters. Tarapchak et al. (1982) showed that bound PO_4-P can be released after a 16-s exposure time to molybdate reagents.

Stainton (1980) reported that ^{32}P-spiked lakewater filtrates from the Canadian Precambrian Shield contained a labeled colloidal fraction. When treated with several variations of the molybdenum blue method followed by Sephadex gel chromatography, this fraction would lose radioactivity, and this was proof that the acid hydrolysis of the colloidal fraction was responsible for the overestimation of the orthophosphate present in the lakewater.

The present study was undertaken to determine whether using the disappearance of the colloidal fraction radioactivity was a conclusive procedure to determine which fraction was responsible for the apparent discrepancy between the molybdenum blue methodology and the Rigler radiobioassay. Emphasis must be placed on the fact that ^{32}P-labeled compounds may not be representative of the molybdenum reactive compounds which are measured directly by chemical procedures. However, radiotracer techniques have the desired sensitivity to assess the effect of the molybdate reagents on recently formed phosphorus substances. The source of the interfering material in the orthophosphate assay is important for two reasons: (1) the identified material can be isolated and checked for biologically available phosphorus, and (2) a selective procedure can be developed which removes the material and renders the molybdenum blue methodology more specific for orthophosphate.

Materials and Methods

Gel chromatography was accomplished using two G-25 "medium" Sephadex (Pharmacia) 2.5 × 35 cm columns. Column 1 was eluted with 0.3% NaCl and 0.02% NaN_3 and Column 2 was eluted with 0.05 mol·L^{-1} NaOH and 0.3% NaCl. The samples were injected onto the columns using a 2.7-mL sample loop that was thoroughly washed with distilled water, methanol, and air-dried before each run. The column effluent was collected in 4.8-mL fractions. Void volume and PO_4 retention volumes were measured using distilled water solutions of blue dextran 2000 (Pharmacia) and $^{32}PO_4$, respectively. ^{32}P activity was measured by Cerenkov counting using a Searle Mark III liquid scintillation counter. Column efficiencies were calculated as the percent of the radioactivity [disintegrations per minute (DPM)] recovered between the eluant volumes of 60–175 mL and the total radioactivity put on the column.

Lakewater was collected from a depth of 1 m in Lake St. George (LSG), a small kettle lake in the Pleistocene kame moraines near Toronto, Ont. The lake was sampled on June 23, 1980 (temperature at 1 m was 24°C, soluble reactive phosphorus was 1 μg·L^{-1}, and total phosphorus was 19 μg·L^{-1}) and November 18, 1982 (temp. = 5°C, SRP = 5.1 μg·L^{-1}, TP = 43.6 μg·L^{-1}). About 0.5 μCi (1 Ci = 37 GBq) carrier-free phosphorus-32 ($^{32}PO_4$) (Amersham) was added and the water incubated at 22°C for 27 h to approach equilibrium of labeled and unlabeled phosphorus in the subsequent fractionation. The sample was then filtered through a 0.45-μm Sartorius membrane filter (SM 11306) into an acid-cleaned flask containing sodium azide to a final concentration of 0.02%. The filtrate was then subjected to various treatments before molecular weight fractionation by gel chromatography.

The hardwater lake filtrates cannot be used immediately after filtration for testing the effect of the molybdate reagents on the ^{32}P-labeled fractions. The research of Yoza et al. (1971) and Yoza (1973) clearly shows that molybdophosphoric acid is strongly adsorbed to Sephadex dextran gels and that quantitative recovery can be achieved using 0.1 M NaOH. Preliminary experiments showed that a precipitate formed in LSG filtrates when the pH was raised to 11–12 (Burnison unpublished data) and the recovery of $^{32}PO_4$ was not quantitative. The presence of Ca^{+2} and Mg^{+2} was thought to be the cause of these low recoveries. The effect of Ca^{+2} at a high pH on the elution of $^{32}PO_4$ was tested by adding $^{32}PO_4$ to a 1.1 mmol·L^{-1} solution of $CaCl_2$ and raising the pH to 11.5 with NaOH. The sample was applied to the G-25 Column 1.

The effect of the Murphy–Riley (1962) reagent on the $^{32}PO_4$ added to distilled water was tested to ensure using $^{32}PO_4$, and the reduced molydbophosphoric acid was not contrary to the observations of Yoza et al. (1971) and Yoza (1973) using reduced molydbophosphoric acid and chemically analyzed for orthophosphate. The Sephadex G-25 elution profiles of $^{32}PO_4$ with and without Murphy–Riley reagent were determined by adding $^{32}PO_4$ to distilled water; one aliquot had the Murphy–Riley reagent added, allowed to stand for 30 min, and injected onto Column 1; in the other aliquot, the pH was raised to 12 and injected onto Column 2.

Interfering cations were removed by passing the lakewater filtrates through a column (30 × 5 mm) of Dowex 50W-X8 Na^+, 100/200 mesh, (Bio-Rad Laboratories). The ^{32}P-elution profile of this sample was compared to a control which had not been exposed to the cation resin. Acidic molybdate reagent (Murphy and Riley 1962) was then added to the eluant from the cation exchange resin. After 30 min the pH was raised to 11.5 with NaOH and an aliquot was applied to Column 2. The control was resin-treated filtrate, without

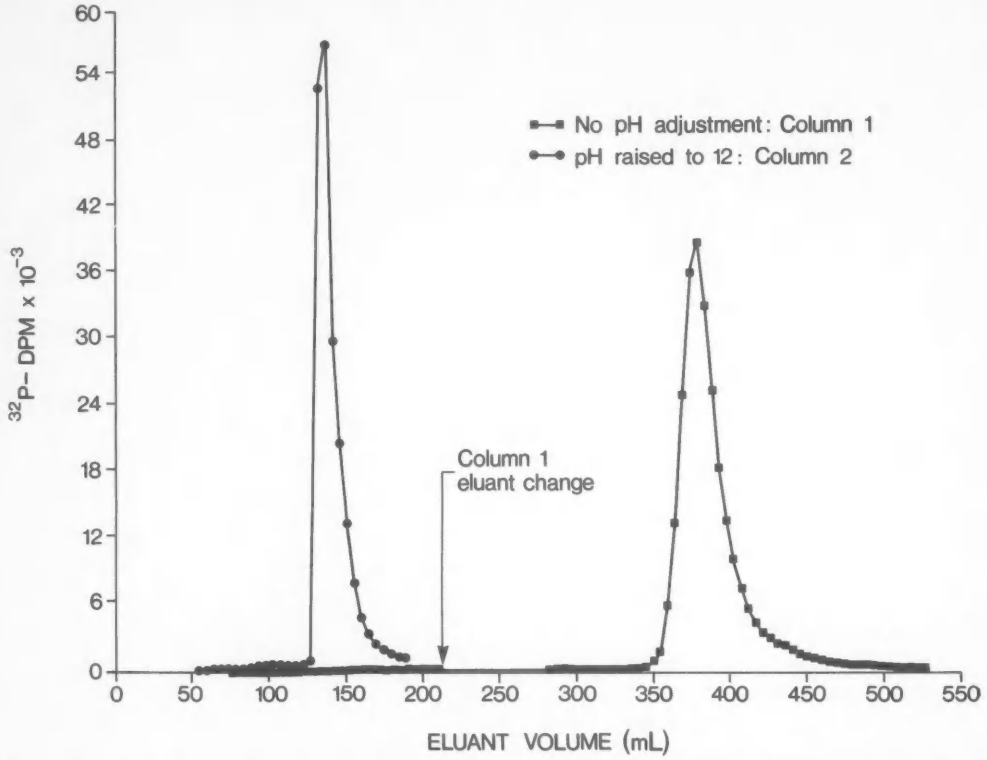

FIG. 1. Adsorption of $^{32}PO_4$ (in distilled water) treated with Murphy–Riley reagent onto Sephadex G-25 Column 1 and subsequent elution with 0.05 mol·L^{-1} NaOH and 0.3% NaCl (■-■); thousands of disintegrations per minute (DPM) are plotted against eluant volume. Elution pattern of $^{32}PO_4$ treated with Murphy–Riley reagent using Sephadex Column 2 (●-●).

added Murphy–Riley reagent, pH raised to 11.5, and an aliquot applied to Column 2.

The chemical composition of the "colloidal" peak is unknown and a simple evaluation of either organic or inorganic composition would be useful in explaining acid hydrolysis observations. The lability of the "colloidal" peak to ultraviolet light combustion was run according to Armstrong et al. (1966) using the ultraviolet photooxidation unit (La Jolla Scientific Co., La Jolla, CA). During this procedure the pH remained at 7.9, the normal pH of the lake water, so inorganic P-containing colloids would not dissolve.

Results and Discussion

Adsorption of Reduced Molybdophosphoric Acid to Dextran Gel

Molybdophosphoric acid is known to be strongly adsorbed to Sephadex dextran gels; it can be dissociated with NaOH and quantitatively recovered (Yoza et al. 1971; Yoza 1973). Figure 1 shows that ^{32}P-labeled reduced molybdophosphoric acid or phosphomolybdenum blue (PMB) is also strongly adsorbed to Sephadex G-25. The ^{32}P-labeled PMB remains at the top of the dextran when NaCl–NaN_3 is used as the eluant. However, when the eluant is switched to 0.05 mol·L^{-1} NaOH and 0.3% NaCl, 92% of the radioactivity is recovered. If the pH of the PMB was raised to between 11 and 12 before being applied to the column and NaOH–NaCl was the eluant, 97% of the applied radioactivity would be recovered from the dextran gel.

Adsorption of ^{32}P-labeled PMB is contrary to the findings reported by Stainton (1980). He reported elution of the PMB using 0.4% NaCl and 0.07% NaN_3. His procedure did not include elution of the molybdenum blue reagent-treated samples at high pH, and the $^{32}PO_4$ activity had to be adsorbed on the dextran gel. Even when neutralized (to pH 7) as was used on some of Stainton's samples, the reduced molybdophosphoric acid complex would not be dissociated (Burnison unpublished data). Some of Stainton's observations are questionable, because of the absorption of the PMB to dextran gels at pH values less than 11. Stainton (1980) states that the behavior of the orthophosphate peak is irrelevant to his main

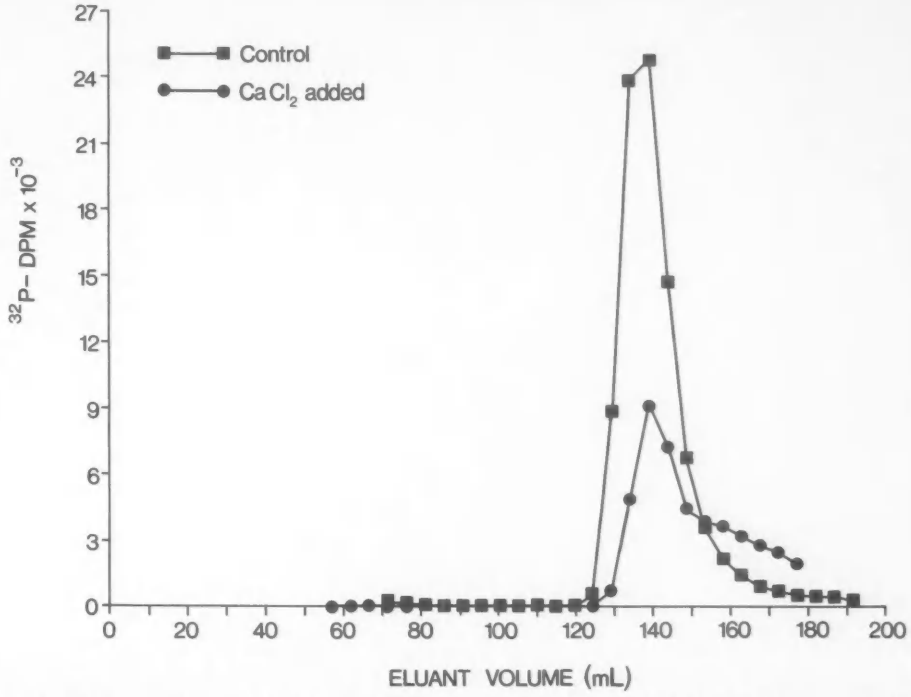

FIG. 2. Effect of presence of 1.1 mmol·L^{-1} $CaCl_2$ at pH 11.9 on elution pattern and recovery of $^{32}PO_4$ (●-●). Elution profile of $^{32}PO_4$ in distilled water raised to pH 11.9 (■-■). Sephadex G-25 Column 1.

argument, which is that the molybdenum blue methods hydrolyze the "colloidal" peak. However, if the PMB is adsorbed to the dextran gel and cannot be removed with a neutral pH eluant, the behavior and radioactivity of the orthophosphate peak becomes very important and an increase in the activity will corroborate the hydrolytic effect of the molybdenum reagents. The disappearance of the "colloid" peak cannot be taken as evidence of acid hydrolysis without an identical increase in the $^{32}PO_4$ peak.

Stainton (1980) had two other interesting observations. In his fig. 6, the $^{32}PO_4$-labeled sample was only treated with HCl (pH = 1.0) and not with the acidic molybdenum reagents. The "colloidal" peak did shift to the orthophosphate position. These data indicate that acid hydrolysis of a very labile organic compound may have occurred or an inorganic particle may have dissociated upon acidification. Alternatively, the "colloidal" ^{32}P-labeled material precipitated in acid and remained at the top of the Sephadex column until the neutral eluant brought it back into solution with subsequent elution around the orthophosphate elution volume. This certainly may have occurred considering that the peak which did elute was very broad compared with the other chromatographed $^{32}PO_4$ peaks. In his fig. 7, the phosphomolybdenum complex was extracted with isobutanol and there was only a small amount of radioactivity left in the aqueous phase. Unfortunately, one has to assume that the remaining activity was quantitatively recovered in the isobutanol layer. Unless proven otherwise, the loss of the "colloidal" peak may be caused by the acid precipitation of the "colloidal" ^{32}P-labeled material. This material could be present at the isobutanol–water interface and such a fraction could have easily been ignored.

EFFECT OF Ca^{+2} AND HIGH PH

When the pH of Lake St. George water was raised (with or without added Murphy–Riley reagent), a noticeable precipitate formed and the recovery of $^{32}PO_4$ was not quantitative. To test the effect of the possible interference of Ca^{+2} ion, $^{32}PO_4$ was added to 1.1 mmol·L^{-1} $CaCl_2$, which is the same concentration of Ca^{+2} as in LSG. The combination of high pH (11.9) and calcium reduced the recovery of the $^{32}PO_4$ from 100% in the pH 11.9 control to 49.2% (Fig. 2). The remaining radioactivity was in a precipitate at the top of the column and could be removed by passing 1 N HCl through the dextran gel. Orthophosphate is known to be precipitated in the presence of Ca^{+2}. The orthophosphate may also be precipitated as $^{32}PO_4$–$CaCl_2$–$Ca(OH)_2$ (Fiske and SubbaRow 1929) or $^{32}PO_4$–calcite (Murphy et al. 1983).

Because Ca^{+2} ions interfere with the gel chromatography of $^{32}PO_4$ at high pH, cations were removed from the ^{32}P-labeled LSG filtrates by ion exchange. The cation resin treatment had

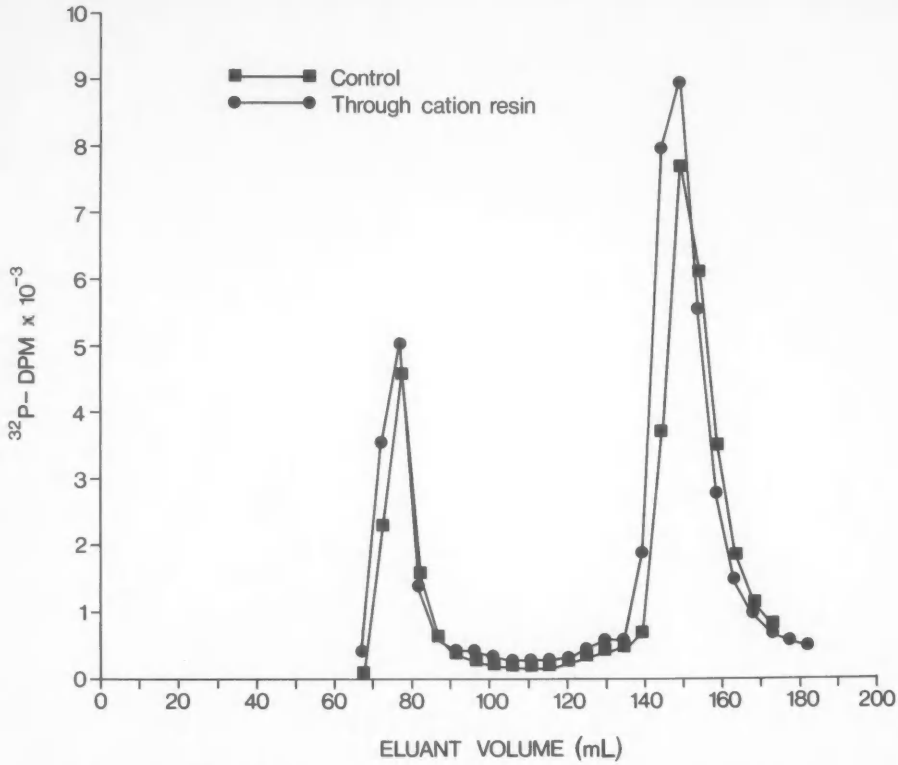

FIG. 3. Effect of cation exchange resin on ^{32}P-activity in Lake St. George filtrate (27-h incubation). Sephadex G-25 Column 1. Control (■-■), through cation resin (●-●), Nov. 18, 1982.

a negligible effect on the elution pattern (Fig. 3). However, the recoveries for the control and through cation resin were 67.6% and 82.8%, respectively. The low recoveries (based on total recovery from 60 to 175 mL) may be caused by a phenomenon of irreversibly absorbed high molecular weight materials (Downes and Paerl 1978), or the retention of an inorganic phosphorus particle, or simply not monitoring the $^{32}PO_4$ tailing. Resin treatment did improve the recovery of ^{32}P-labeled materials, and the relative radioactivities between the "colloidal" and $^{32}PO_4$ peaks are similar.

ACID HYDROLYSIS OF "COLLOIDAL"-P

Stainton (1980) reported 60% of the colloid-P formed in a softwater lake was acid hydrolyzed by the Murphy–Riley reagent within 10 min. However, the same reagent given 30 min did not hydrolyze a significant amount of the "colloidal"-P formed in LSG, a hardwater lake (Fig. 4). The modifications added to the procedure used by Stainton (1980) are necessary to obtain quantitative recovery of the PMB. The recovery of radioactivity in both the control (resin-treated) and the aliquot treated with Murphy–Riley reagent was quantitative (103%). The $^{32}PO_4$ peak in the control run was eluted ahead of the sample which contained the Murphy–Riley reagent when NaOH–NaCl was used as the eluant. The reason for this is unknown, but it may be an ionic repulsion phenomenon because the orthophosphate is near its third dissociation constant at pH 12.7 (Weast 1971). This charge may be lessened in the presence of the various cations present in the Murphy–Riley reagent. As the control includes some mid-range ^{32}P-labeled material (eluant volume 105–130 mL), the Murphy–Riley reagent sample must include these fractions. Therefore, the ^{32}P-activities for the orthophosphate peaks in the control and the Murphy–Riley (M–R) sample are 73.2 and 73.6%, respectively. If the mid-range fractions were not included in the M–R sample, then the integrated activity would be 67.3% or very close to the orthophosphate peaks in Fig. 3 (66.0 and 68.2%). These values show that, at least in the LSG sample of November 18, 1982, the acidic Murphy–Riley reagent did not hydrolyze the "colloidal" ^{32}P-labeled components. An identical experiment was run on June 23, 1980. On that date (Table 1), the "colloidal" peak was reduced by 13.3% and the orthophosphate peak was increased by 13.5% upon treatment with the Murphy–Riley

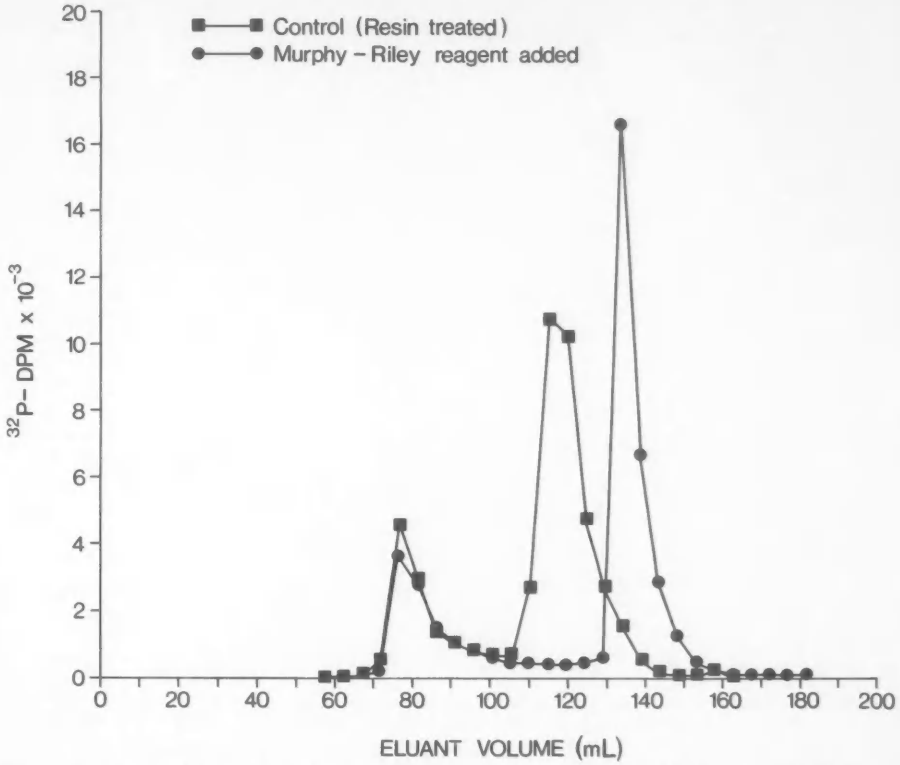

FIG. 4. ^{32}P-activity in 27-h Lake St. George filtrate (cation exchange resin treated) before (■-■) and after (●-●) treatment with Murphy–Riley reagent. Sephadex G-25 Column 2, Nov. 18, 1982.

TABLE 1. Effect of Murphy–Riley reagent on Lake St. George water. Sample collected on June 23, 1980.

Percent of total recovered radioactivity		
Treatment	"Colloidal"-P	$^{32}PO_4$
Passed through Dowex 50W-X8; applied to Column 1	87.9	11.7
Passed through Dowex 50W-X8; Murphy–Riley reagent added; pH adjusted to 11.8; applied to Column 2	74.6	25.2

TABLE 2. Reactivity of phosphate minerals with Murphy–Riley (M–R) reagent.

Mineral	Total P,[a] mg·g^{-1}	HCl extract,[a] mg·g^{-1}	M–R reactive, mg·g^{-1}
Fluoroapatite	166	152	177
Chloroapatite	159	152	169
Francolite	84	40	39
Dahlite	134	119	147
Quercyite	111	102	100
Colophane	140	129	139
Variscite	156	2	4

[a]From Williams et al. (1980).

reagent. Obviously, during this period there was some acid hydrolysis of the "colloidal" material, but most of the peak was acid stable.

APATITE INTERFERENCE WITH ORTHOPHOSPHATE ANALYSES

Mass balance data of soluble reactive phosphorus in lakewater filtrate suggested that much of it may be present as a particulate (Chamberlain and Shapiro 1973; Tarapchak et al. 1982). Reid et al. (1980) stated that as much as one-third of the "dissolved" (<0.45 μm) inorganic phosphorus load in Kamloops Lake, B.C., is apatite. Known phosphate minerals do react with the Murphy–Riley reagent (Table 2). The varieties of apatite tested contained phosphorus concentrations, as tested by the Murphy–Riley method, equivalent to the concentration found in these minerals by HCl extraction which had been previously extracted with dithionite–citrate–bicarbonate (DCB) and NaOH (Williams et al. 1980).

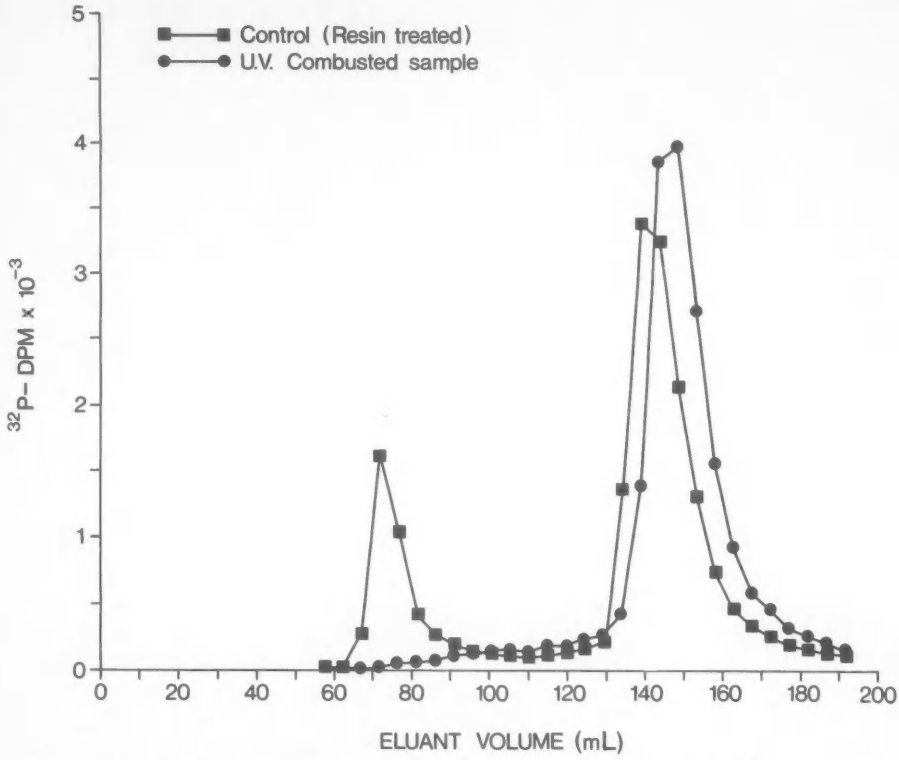

FIG. 5. ^{32}P-activity in 27-h Lake St. George filtrate (cation exchange resin treated) before (■-■) and after (●-●) ultraviolet light irradiation. Sephadex G-25 Column 1, Nov. 18, 1982.

The nonapatite phosphate mineral, variscite, did not react with the Murphy–Riley reagent, as expected. These minerals had been ground to a particle size of ~250 μm and therefore are not soluble, but under natural conditions apatite particles could be eroded to particles of <0.45 μm.

Smith et al. (1978) have shown that ground apatite may provide a source of orthophosphate for bacteria and algae. However, Williams et al. (1980) dispute this view and feel that natural apatite is unavailable to microorganisms, but that nonapatite inorganic phosphorus is correlated to phosphorus uptake. The suggestion that soluble phosphorus may merely be adsorbed onto high molecular weight colloidal material is still a possibility (Westland and Boisclair 1974). Therefore, inorganic particles (<0.45 μm) may or may not be used by microorganisms, but if the particles contain apatite they will react with the molybdenum blue tests.

COMBUSTION OF "COLLOIDAL"-P BY UV LIGHT

The identity of the "colloidal" substances which disappear from the Sephadex void volume fraction would help us understand the acid effects. Ultraviolet light combustion is a good indicator whether a substance is organic. The void volume material in the 1982 LSG sample was organic (Fig. 5). The "colloidal" peak was destroyed by the UV combustion and the radioactivity which was lost (18.4% of total recovered) was accounted for in the $^{32}PO_4$ peak (18.5%). As the pH of the combusted sample remained at pH 7.9, any inorganic phosphorus-containing complex should have remained intact. If the "colloidal" peak had not been decreased, the radioactivity would be considered an inorganic particle or complex which would most likely be dissolved by acid in the Murphy–Riley procedure. This inorganic complex may eventually be available to microorganisms under slightly acidic microenvironmental conditions. The orthophosphate could also have been absorbed onto an organic colloidal material (Westland and Boisclair 1974), and this association would be destroyed by UV combustion. The bioavailability of this phosphorus, however, is unknown.

"Colloidal"-P materials, in lakes, which undergo acid hydrolysis, will most likely vary in concentration dependent upon lake type, land drainage, and seasonable temperatures. If there are inorganic phosphorus-containing "colloids" present, these should readily release orthophosphate when the pH is lowered. Organic "colloids" will vary in their acid lability. In conclusion, because of the complexity of "colloidal" mate-

rials in different bodies of water, a general statement on the usefulness of the molybdenum blue methods for the determination of biologically available phosphorus cannot be made and an accurate bioavailable phosphorus (BAP) assay, which can be used routinely in the laboratory, is needed. Ideally, a method which can quickly partition "colloidal" material from orthophosphate seems to be the best avenue for future research.

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Ceratomyxa shasta: Longevity, Distribution, Timing, and Abundance of the Infective Stage in Central Oregon

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Characteristics of the infective stage of *Ceratomyxa shasta* were studied in the Deschutes River of central Oregon from 1972 through 1981. The infective stage remained viable <10 d in Deschutes River water maintained in aerated, river-temperature-controlled aquaria. Live-cage exposures of susceptible rainbow trout (*Salmo gairdneri*) indicated that infectious *C. shasta* emanate from the bottoms of two reservoirs. Epilimnions of both reservoirs did not contain the infective stage during thermally stratified periods. Infectious *C. shasta* originating in one reservoir passed down the Deschutes and Columbia rivers. During spring and summer, infectious *C. shasta* in the other reservoir did not reach the outlet, located 56 m above the bottom. In the Deschutes River, the infective period began before March 31 in 1978, between April 3 and 10 in 1979, and between April 16 and 23 in 1981 when river temperatures were between 6.9 and 8.6°C. Consecutive exposures of trout to the same water in aquaria indicated that all infectious *C. shasta* were removed or inactivated during initial exposures. Progressively doubling numbers of test fish exposed in different aquaria showed that one *C. shasta* is capable of causing the death of one susceptible fingerling rainbow trout. Peak abundance of *C. shasta* in Deschutes River water during 1979 was estimated at 148 infectious units/m^3 on June 4. Abundance decreased significantly between 1978 and 1981, presumably because of elimination of ceratomyxosis-caused deaths of hatchery rainbow trout and associated spore deposition in one reservoir. Both the formation of reservoirs and liberation of susceptible host fish can lead to an increased number of *C. shasta*, and result in serious *C. shasta*-induced losses in native salmonid populations.

RATLIFF, D. E. 1983. *Ceratomyxa shasta*: longevity, distribution, timing, and abundance of the infective stage in central Oregon. Can. J. Fish. Aquat. Sci. 40: 1622–1632.

De 1972 à 1981 inclusivement, les caractéristiques du stade infectieux de *Ceratomyxa shasta* ont été étudiées dans la rivière Deschutes, en Orégon central. Le stade infectieux est demeuré viable moins de 10 jours dans de l'eau de cette rivière maintenue dans des aquariums aérés et à température ajustée à celle de la rivière. Des expositions en cages de truites arc-en-ciel (*Salmo gairdneri*) susceptibles montrent que *C. shasta* infectieux provenait du fond de deux réservoirs. Les épilimnions des deux ne contenaient pas de stades infectieux en périodes de stratification thermique. *Ceratomyxa shasta* infectieux provenant d'un réservoir est descendu dans la rivière Deschutes et le fleuve Columbia. Au printemps et en été, l'organisme infectieux de l'autre réservoir n'a pas atteint l'émissaire, situé à 50 m au-dessus du fond. Dans la rivière Deschutes, la période infectieuse débuta avant le 31 mars en 1978, entre les 3 et 10 avril en 1979 et entre les 16 et 23 avril en 1981, alors que les températures de la rivière étaient comprises entre 6,9 et 8,6°C. Après expositions consécutives de truites à la même eau en aquarium, on a constaté que les *C. shasta* infectieux avaient été éliminés ou rendus inactifs au cours des expositions initiales. En doublant progressivement le nombre de poissons expérimentaux exposés dans différents aquariums, on a constaté qu'un *C. shasta* peut causer la mort d'une truite arc-en-ciel de la grosseur du doigt et qui est sensible. On a estimé à 148 unités infectieuses par mètre cube le 4 juin la densité maximale de *C. shasta* dans la rivière Deschutes en 1979. Entre 1978 et 1981, *C. shasta* devint nettement moins abondant, probablement à cause de l'élimination des mortalités de truites arc-en-ciel d'élevage dues à la cératomyxose et de la déposition qui lui est associée des spores dans un réservoir. La formation de réservoirs et la mise en liberté de poissons hôtes susceptibles peuvent toutes deux contribuer à une augmentation de *C. shasta* et occasionner de sérieuses pertes parmi les populations de salmonidés indigènes.

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THIS paper describes the longevity of the infective stage of *Ceratomyxa shasta* in the aquatic environment, distribution, and the annual initial timing of the infective period for this parasite in the lower Deschutes River (Oregon), and a bioassay technique to estimate the abundance of the infective stage in natural waters. Abundance in the lower Deschutes River was estimated periodically during the spring, summer, and fall of 1979. Changes in abundance were monitored from 1978 through 1981.

The life history of the histozoic myxosporean parasite of salmonids, *Ceratomyxa shasta*, has not been described. Its distribution is restricted to certain waters of western North America (Johnson et al. 1979). Noble (1950) described several life stages, culminating in a spore stage, which occur inside the host during advanced infections. The spore stage is thought to be the infective stage for some myxosporeans (Halliday 1976); however, this has not been demonstrated with *C. shasta*. Neither feeding spores to susceptible individuals nor close association between susceptible and diseased fish shedding spores have resulted in transmission (Schafer 1968; Fryer and Sanders 1970). Infections have been produced by intraperitoneal injection of trophozoites from diseased fish into healthy fish (Johnson 1975). Natural infections result only when susceptible individuals are exposed to waters containing the undescribed infective stage.

Sanders et al. (1970) found the infective stage was present in the mainstream Deschutes River (Oregon) below its confluence with the Little Deschutes River. However, when I exposed susceptible test fish in hydroelectric reservoirs of the lower Deschutes River in 1972, the infective stage was not encountered at several locations even though it was found to enter and leave the reservoirs. Johnson (1975) investigated the viability of the infective stage and found that it survived only 3 d when infective water was placed in a sealed container. I hypothesized that a short longevity might explain its absence in certain reservoir waters.

Although the infective stage has not been identified, it is known to occur seasonally (demonstrated by infections in test fish), appearing in the spring as the water temperature approaches 10°C and continuing until late fall or early winter (Schafer 1968; Johnson 1975). The initial timing of the infective period in the Deschutes River is important because hatchery-reared anadromous salmonids are released in spring and must emigrate through waters potentially containing the infective stage (Ratliff 1981). Because of difficulties in identification, no method has previously been described to quantify the numbers of infectious units in the aquatic environment.

Methods

STUDY AREA

The Deschutes River of Oregon flows east from the Cascade Mountains and then north ~300 km to enter the Columbia River 327 km upstream from the Pacific Ocean. The study area included a portion of the river near the Pelton Hydroelectric Project from 161 to 191 km above confluence with the Columbia River (Fig. 1). Pelton Dam and Pelton Regulating Dam (for regulating downstream flows) were constructed in 1958. Round Butte Dam was constructed immediately upstream from the backwater of Pelton Dam in 1964. The three resultant reservoirs are physically quite different. The regulating reservoir is homothermal, 5.1 km long, and has a maximum depth of 15 m, but varies greatly in depth and volume with power production and associated discharge upstream. Lake Simtustus (Pelton Reservoir) is 11.3 km long and relatively narrow with little shoal area. It has a storage capacity of 41 Mm^3, a surface area of 274 ha, and a maximum depth of 51 m. The outlet (Pelton Dam intake) is located near the bottom and deepest part of the reservoir. Lake Billy Chinook (Round Butte Reservoir) has a storage capacity of 650 Mm^3, a surface area of 1619 ha, and a maximum depth of 127 m (Mullarkey 1967). In addition to inundating 13.7 km of the Deschutes River Canyon, Lake Billy Chinook extends up two major tributaries, inundating 9.7 km of the Crooked River and 19.3 km of the Metolius River (Fig. 1). Because Round Butte Dam was constructed of earth-and-rock fill, the outlet of Lake Billy Chinook is located upstream and laterally from the dam on a rock point of the flooded canyon slope, 56 m above the bottom and 71 m from the surface.

Both Lake Simtustus and Lake Billy Chinook become thermally stratified during late spring and summer with surface temperatures of ~21°C. As both reservoirs have hypolimnic outlets, epilimnions are permanent until fall turnover, which normally occurs in October. The Deschutes River temperature below the dams varied from ~5 to 14°C yearly during the study period. Discharge flows averaged 140 m^3/s.

The infective stage of *C. shasta* was first detected in Oregon in 1965 when salmonids were reared in Deschutes River water immediately below the Pelton Regulating Dam (Conrad and Decew 1966). Its presence at this site has been demonstrated each year since 1965 (Sanders et al. 1972; Ratliff 1981). Sanders et al. (1970) showed the infective stage to be present in the Deschutes and Crooked rivers where they enter Lake Billy Chinook (Fig. 1). Later, it was also detected in the Metolius River (Johnson et al. 1979).

TEST FISH AND DIAGNOSIS OF CERATOMYXOSIS

Finglerling rainbow trout (*Salmo gairdneri*) of Oak Springs and Roaring River Hatchery stocks (Kinunen and Moring 1978) were obtained from various state hatcheries in central Oregon. These stocks were chosen because they are highly susceptible to ceratomyxosis (Johnson 1975; Udey et al. 1975). Test fish used during late summer and fall were Oak Springs stock, one generation removed, from gametes taken at Diamond Lake (Oregon). In Diamond Lake, very cold water delays spawning from the normal fall period until May. This allowed for small (1−4 g) test fish of similar stocks throughout the infective period for *C. shasta*.

Test fish were not fed during exposure to *C. shasta*, but were fed an Oregon Moist Pellet diet after exposure during the holding (incubation) periods. The antibiotic oxytetracycline in the form of TM-50 (Pfizer) was added (3% level) when available to decrease interference from bacterial pathogens. No chemotherapeutic agent has been found effective in preventing or arresting ceratomyxosis (Sanders et al. 1972).

Dead fish were considered infected if one or more spores of *C. shasta* were found during a 5-min microscopic search

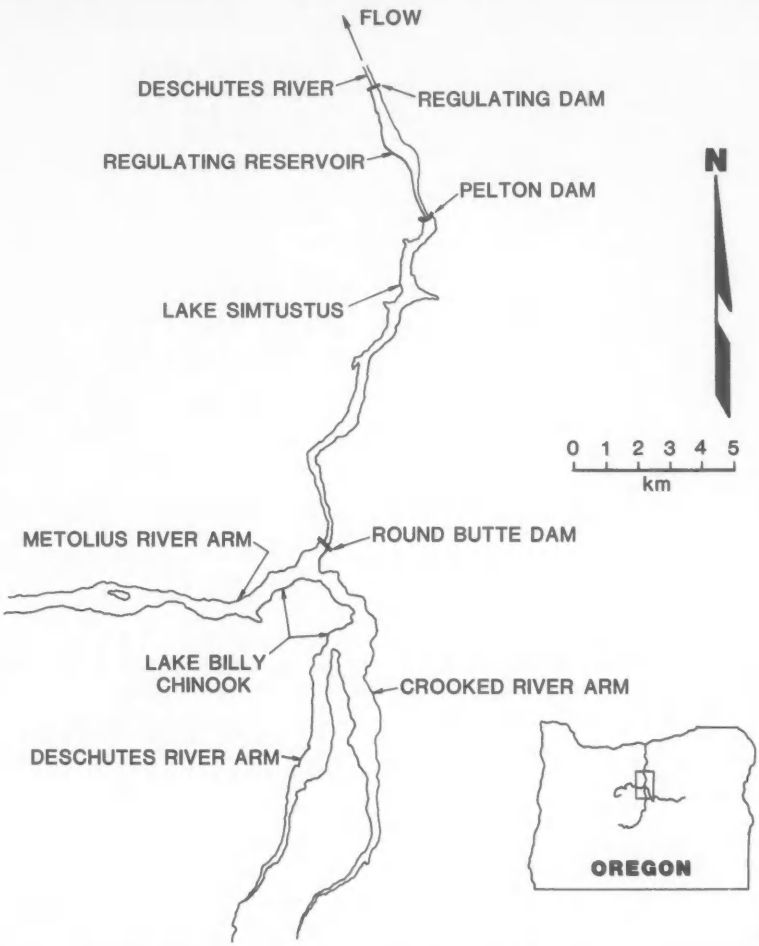

FIG. 1. Location of study area in the Deschutes River Basin of central Oregon.

(100−400×) of wet-mounted material scraped from inside the hind gut with a wire loop. After mortality subsided in each experiment (~100 d), samples were taken and examined microscopically from fish showing signs of ceratomyxosis.

LONGEVITY

Water known to contain the infective stage of *C. shasta* was pumped from the Deschutes River below the Pelton Regulating Dam into circular, 94.6-L polyethylene aquaria. The water was aerated using a standard aquarium air pump with one air stone per aquarium. Aquaria were covered and partially immersed in a 1.8-m-diameter tank containing a continuous flow of Deschutes River water to control temperature. They were exposed to natural light but no direct sunlight.

Infective water was collected August 29, 1978, in each of five aquaria. Five groups of test fish (n = 39−75 per group), with a mean weight of 3.0 g, August 29, were exposed, one group per aquarium, for 48 h after the water had been held for periods of 0, 3, 11, 30, or 60 d. In addition, other groups of fish were given 48-h exposures to 0-d water aquarium at 3, 11, 30, and 60 d from the initial water-holding date to determine if the water retained infectivity after contact with susceptible host fish. After exposure, test groups were uniquely fin-marked for later identification and transferred into 0.9-m-diameter circular tanks supplied with at least 4 L/min of 10°C water free of the infective stage. All but two of the test groups were held until January 18, 1979 ($T \geq 112$ d from initial exposure). The 60-d groups were held until February 5, 1979 (T = 100 d).

A second trial was conducted in 1979 using water held for generally shorter durations. Infective water was drawn from the Deschutes River and placed in 10 aquaria May 25. Ten test groups of 40 fish each were exposed, one group per aquarium, for 96 h after holding intervals of 0 through 7, 10, and 14 d. An additional group was exposed (96 h) to water in the 0-d interval aquarium immediately following the first 96-h exposure. Timing of this exposure coincided with the 4-d exposure.

Distribution

To determine distribution of the infective stage, I exposed susceptible test animals to various waters for a short duration (~7 d), and then transferred them into a water supply free of *C. shasta*. Test fish were exposed in either 5.7-L plastic buckets (covered with nylon netting), 22.7-L plastic buckets, or in 60- by 45-cm cylindrical cages with 5-mm aluminum mesh.

Vertical distribution of the infective stage in Lake Simtustus was determined by attaching live cages to a rope at intervals corresponding to different exposure depths. About eight test fish were exposed at each of seven depths from the surface to 39.6 m in tests conducted July 22–29 in 1974 and June 26–July 3 in 1975. Live cages were covered with plastic bags by divers before being lowered and raised to prevent exposure to water at other levels. In tests conducted in 1979, ~35 test fish were exposed at each depth. One test was conducted September 20–27 when the reservoir was thermally stratified and a second conducted October 29–November 5 after the reservoir had become homothermous. Live cages were not covered with plastic bags in 1979. Water temperatures were monitored at the various levels during each exposure.

Annual Initial Timing

To determine the beginning of the infective period for *C. shasta* in the lower Deschutes River, I exposed susceptible rainbow trout for 7-d periods at two locations during the springs of 1978 and 1979, and one location in the spring of 1981. Live cages containing test fish were placed 1 km above confluence with the Columbia River (Moody), and just below the Pelton Regulating Dam (km 161). In 1978, 70–100 fingerlings were exposed each week between March 31 and June 1. In 1979, ~50 test fish were exposed each week between March 13 and May 21. Exposures in 1981 were conducted only at the upper site (km 161) every other week between March 31 and July 3, using ~50 test fish each time. River flows and temperatures were recorded during each exposure. After exposure, test fish were given unique fin marks and placed in 0.9-m-diameter circular tanks (10°C water). Mortalities were removed daily and every third one was assayed for the presence of *C. shasta*. Infection frequencies were compared between times, locations, and years.

Abundance

After longevity experiments indicated that the infective stage does not reproduce itself directly and that all infectious units in test aquaria are removed or neutralized by the susceptible test fish, I hypothesized that the number of resulting infections could be used as an index to the number of infectious organisms present during the exposure. However, this necessitated determining how many infective organisms are necessary to cause infection and disease (i.e. organisms per infectious unit). This was done by greatly increasing the density of susceptible fish exposed to a standard volume of infective water. The change in incidence of disease with density was used to indicate if one or many infectious *C. shasta* were required to establish an infection.

Exposure-density tests were done by collecting infective water in six 94.6-L aquaria as described in the longevity experiments. Five test fish were exposed in the first aquarium and the number progressively doubled until 160 fish were exposed in the sixth. The first trial was conducted May 25–29, 1979, with Roaring River trout averaging 2.3 g. The second trial was conducted September 26–30, 1979, with Oak Springs trout averaging 1.6 g.

To determine the relative abundance of the infective stage over the infective period in 1979, I periodically exposed 40 test fish to 94.6 L of Deschutes River water for 96 h as described above. Three replicate groups were exposed every 3 wk from March 15 until November 26. After exposure, each replicate group was held (10°C) in a separate 0.9-m-diameter tank.

Liberations of susceptible rainbow trout into Lake Simtustus were terminated in 1977. Exposures, similar to those in 1979, were conducted in 1980 and 1981 to determine if a change in abundance of infectious units would follow the restriction of susceptible hosts. In 1980, exposures were made in late July only. In 1981, comparable exposures were made monthly May through August.

Results

Longevity

No infections were observed in test fish after exposure to Deschutes River water that had been maintained in aquaria for 10 or more days in 1978 or 1979 (Table 1). The presence of another pathogen (*Costia* sp.) in 1978 partially masked results by causing mortality in most groups prior to completion of the incubation period for *C. shasta*. Nevertheless, 27 and 6 of the remaining test fish developed ceratomyxosis after exposure to water that had been maintained 0 and 3 d, respectively. In 1979 there was general reduction in the number of infections as the preexposure maintenance time increased to 7 d.

Test fish exposed to water in which susceptible fish had previously been exposed did not contract *C. shasta* (Table 1). However, test fish exposed in aquaria where Deschutes River water had been maintained for the same 3-d or 4-d intervals, but with no fish, became infected. These results indicate the susceptible trout in the initial exposures removed or neutralized all infectious units in the aquaria.

Distribution

Waters downstream from Lake Simtustus contained the

TABLE 1. Infection frequencies from *Ceratomyxa shasta* in susceptible rainbow trout fingerlings after exposure to Deschutes River water previously maintained in aquaria for various times.

Days maintained[a]	Positive deaths / negative deaths[b]	Survivors	Infection frequency (%)
From Aug. 29, 1978			
0	27/9	39	36
3	6/16	47	9
3[c]	0/14	54	0
11	0/17	39	0
30	0/23	29	0
60	0/0	43	0
From May 25, 1979			
0	20/1	19	50
1	13/1	26	33
2	4/1	35	10
3	8/1	31	20
4	5/1	17[d]	23
4[c]	0/0	22[d]	0
5	9/0	30	23
6	3/0	37	8
7	1/0	38	3
10	0/0	40	0
14	0/0	40	0

[a]Prior to the introduction of test fish.

[b]In 1978, some fish died of *Costia* sp. infection during the incubation period for *Ceratomyxa shasta* and are included under negative deaths.

[c]These exposures were made to the same waters as the 0-d exposures. In 1978, subsequent exposures in the same water, coinciding with each of the longer holding-interval exposures, also produced no infection.

[d]Some fish died during marking and transfer to the incubation tanks.

TABLE 2. Infection frequencies from *Ceratomyxa shasta* in susceptible rainbow trout exposed to various waters of the lower Deschutes River and associated reservoirs, listed downstream to upstream (See Fig. 1).

Exposure site	Exposure dates	Mean temp. (°C)	No. infected / No. exposed	Frequency (%)
Lower Deschutes River (km 161)[a]	Sept. 1–6, 1976	13	27/27	100
Pelton Dam discharge	July 22–29, 1974	12	5/7	71
Lower Lake Simtustus	See Table 3			
Willow Creek inflow	Aug. 20–27, 1973	18	0/7	0
Round Butte Dam discharge[b]	April 16–Jul 1, 1975[c]	6–11	0/55	0
	Sept. 4–15, 1975	13	3/73	4
	Sept. 1, 1976–April 20, 1977[d]	13–5	8/50	16
Lake Billy Chinook				
Near Round Butte Dam, surface	June 26–July 3, 1975	18	0/10	0
Near Round Butte Dam, 50 m	Sept. 4–15, 1975	13	0/100	0
Upper Descutes River Arm, surface	Nov. 4–13, 1975	11	0/29	0
Upper Deschutes River Arm near benthos, 43 m	Sept. 19–26, 1979	11	3/39	8
Deschutes River inflow[e]	Sept. 4–13, 1975	13	61/100	61
Upper Crooked River Arm near benthos, 43 m	Sept. 19–26, 1979	12	14/46	30
Crooked River inflow	Sept. 19–26, 1979	13	37/46	80
Upper Metolius River Arm near benthos, 43 m	Sept. 19–26, 1979	10	0/49	0
Metolius River inflow	Sept. 19–26, 1979	9	0/49	0

[a]In many repeated exposures, *C. shasta* has always caused infections at this site from May through October.

[b]In repeated exposures, April through August, 1972 through 1976, no infections were observed.

[c]Five test fish were transferred weekly into incubation facilities.

[d]Exposure was continuous during these 8 mo.

[e]Infections were observed in each of four exposures at this site.

TABLE 3. Infection frequencies from *Ceratomyxa shasta* in susceptible rainbow trout exposed for 7-d intervals at various depths in lower Lake Simtustus during 1974, 1975, and 1979.

Exposure depth (m)	July 22–29, 1974			June 26–July 3, 1975			Sept. 20–27, 1979			Oct. 29–Nov. 5, 1979		
	Infected total	(%)	Temp. (°C)	Infected total	(%)	Temp. (°C)	Infected total	(%)	Temp. (°C)	Infected total	(%)	Temp. (°C)
0[a]	0/7	(0)	22.2	0/9	(0)	16.1	1/35	(3)	19.4	9/43	(21)	11.7
1.5	0/8	(0)	18.3	0/9	(0)	15.0	0/27	(0)	17.2	7/41	(17)	11.7
4.6[b]	1/7	(14)	13.3	0/7	(0)	12.2	0/45	(0)	14.4	14/45	(31)	11.7
7.6	4/7	(57)	12.2	0/8	(0)	12.2	1/35	(3)	13.9	5/37	(14)	11.7
15.2	3/7	(43)	12.2	4/9	(44)	10.5	4/33	(12)	12.7	8/40	(20)	11.7
22.9	8/8	(100)	12.2	—	—	—	8/39	(21)	12.7	7/35	(20)	11.7
39.6	7/8	(87)	12.2	—	—	—	8/37	(22)	12.7	8/39	(21)	11.7

[a]Repeated exposures of susceptible fish to surface waters of Lake Simtustus during the summers of 1972 and 1973 also produced no infections.

[b]During warm months, the thermocline normally occurred at ~5 m in depth.

infective stage of *C. shasta* throughout its normal infective period (Table 2). Susceptible trout exposed to surface waters of Lake Simtustus during the warm months of 1972 and 1973 when the reservoir was thermally stratified did not contract *C. shasta*. By exposing test fish in vertically suspended live cages in the summers of 1974, 1975, and 1979, the infective stage was found to be present only in the hypolimnion (Table 3). Thermally induced mixing of the reservoir in the fall brought the infective stage to the surface. The one infection occurring in the group exposed at the surface in September 1979 may have resulted from a small amount of cross-contamination of water during transport.

Waters immediately below Lake Billy Chinook (Round Butte Dam discharge) did not contain the infective stage during the normal late spring and summer infective period (Table 2). Repeated exposures from April through August 1972–76 produced no infections. However, exposures in September 1975 and from September 1976 through April 1977 did produce a low incidence.

Test fish exposed at the surface or at 50-m depth in lower Lake Billy Chinook during summer 1975 did not contract *C. shasta* (Table 2). Fish exposed in the upper portions of the Deschutes and Crooked River arms (43-m depth, near bottom) became infected, but those exposed in the Metolius River arm did not. Similarly, the infective stage was present in the Deschutes and Crooked rivers where they enter Lake Billy Chinook, but was not detected in the Metolius River.

ANNUAL INITIAL TIMING

Initiation of the infective period at the Pelton Regulating Dam (km 161) varied from sometime prior to March 31 in 1978 to between April 16 and 23 in 1981 (Fig. 2). In 1978, the infective period had apparently begun prior to the first exposure because 38% of the initial test group exposed between March 31 and April 7 became infected. The earliest that fish became infected in 1978 was April 3–10, when 2 of 48 developed ceratomyxosis. In 1981, the first infection was found in one of 60 fish exposed April 16–23. Initial timing of the infective stage was similar at the Moody site (km 1) in 1978 and 1979.

River temperatures at which test fish first encountered the infective stage varied between years and sites (Fig. 2). In 1978 fish became infected during the March 31 to April 7 exposure when mean temperatures were 9.6°C at the km 1 site and 6.9°C at the km 161 site. In 1979 the temperature averaged 9.7 and 7.7°C at the km 1 and km 161 sites, respectively, when first infections occurred. In 1981 the mean river temperature was 8.6°C during the first infective exposure at km 161.

After the infective period began, infection frequency in subsequent exposure groups generally increased with increasing water temperatures (Fig. 2). Mean time until death varied from ~45–90 d, but generally decreased in later exposures made during periods of higher water temperatures when groups also suffered higher infection frequencies (Fig. 3). Pooling all data, mean time until death was correlated more with infection frequency ($r = -0.81$) than with exposure temperature ($r = -0.44$).

ABUNDANCE

In both trials, a similar number — note — not % of infections was found from each aquarium when numbers of test fish were progressively doubled from 20 to 160 (Table 4). In the first trial (May 25, 1979) there were ~10 infections per aquarium, and in the second (September 26, 1979) there were about four. Because the number of infections observed did not decrease when more test fish were exposed, individual infectious *C. shasta* appear capable of causing ceratomyxosis and death in highly susceptible fingerling trout.

Dead fish from these trials characteristically exhibited more localized gross pathology. In contrast to normal infections, few spores were present and many of those observed were deformed. Occasionally, one side of a spore was completely degenerated or not formed, leaving a nearly oval "half-spore" containing one polar capsule.

In 1979, the infective stage of *C. shasta* was first detected in the lower Deschutes River (km 161) April 26 at an estimated level of 28 infectious *C. shasta*/m^3 (Table 5). Abundance increased in samples from that time until June 4 when a peak level of 148 *C. shasta*/m^3 was estimated. Concentrations were relatively constant (35–74 *C. shasta*/m^3) from the end of June through September, and then decreased through

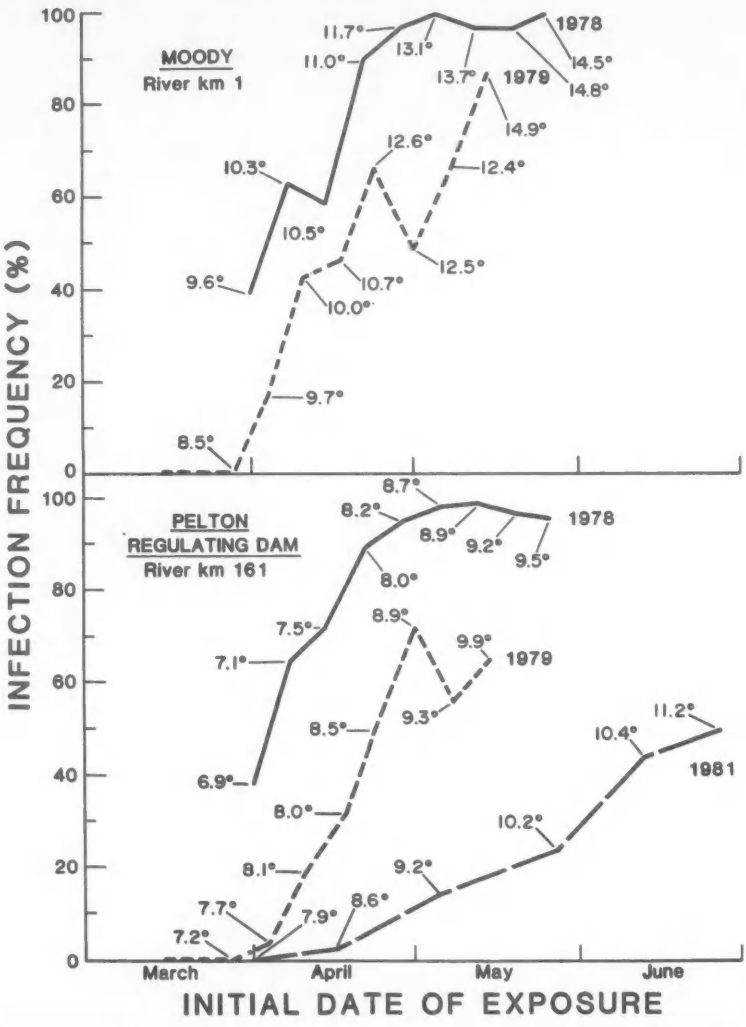

FIG. 2. Infection frequency from *Ceratomyxa shasta* vs. exposure date for test groups of rainbow trout (*Salmo gairdneri*). Exposures were in the Deschutes River at Moody (km 1) or at the Pelton Regulating Dam (km 161) for 7-d periods during 1978, 1979, or 1981. Mean river temperature during exposure is shown near each data point.

the last exposures November 26 (4 *C. shasta*/m^3). There was no apparent correlation between temperature or flow and abundance. Water temperatures increased through July and August (Table 5), and flows were relatively constant from June to October.

Abundance of infectious *C. shasta* decreased between 1979 and 1981. Exposures made in July 1980 produced no infections. In 1981 abundance peaked in June, but at a reduced level compared to 1979 and then decreased sharply (Table 5). Four *C. shasta*/m^3 were estimated on July 20, 1981 compared to 42 on July 16, 1979, and none was detected on August 16, 1981, compared to 74 on August 6, and 56 on September 4, in 1979.

Results from the first trial of the longevity experiment conducted August 29, 1978, indicate a reduction also may have occurred from 1978 to 1979. Twenty-seven infections (285 *C. shasta*/m^3) were found after an exposure to 94.6 L of Deschutes River water. This compares to a mean of 5.3 infec-

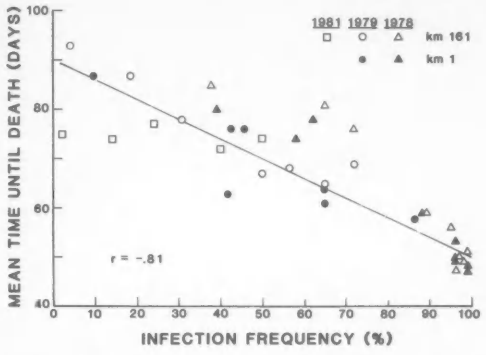

FIG. 3. Mean time until death vs. infection frequency from *Ceratomyxa shasta* for 37 test groups of rainbow trout (*Salmo gairdneri*). Fish were exposed in the Deschutes River for 7 d during the springs of 1978, 1979, or 1981 and then held at 10°C during the incubation period. The line represents a least squares fit.

tions (56 *C. shasta*/m^3) on September 4, 1979. Results of the timing exposures when fish were held directly in the Deschutes River also indicate a significant reduction in the numbers of infectious *C. shasta* between 1978 and 1981 (Fig. 2). This apparent decrease coincides with the termination of liberations of susceptible trout into Lake Simtustus in 1977.

Discussion

LONGEVITY

Test aquaria were designed to simulate the lotic environment by controlling temperature and adding aeration. However, under these conditions no infectivity could be demonstrated after 10 d. Because the infectious units most likely emanated from the benthos of Lake Simtustus within 3 d previous to the experiment, maximum estimated longevity at 11°C was 13 d. The free infectious *C. shasta* apparently must encounter and infect a susceptible host rather quickly, or perish. Although the spore stage of myxosporeans may retain viability for a number of years (Hoffman and Putz 1969), studies have not been reported on the longevity of the infective stage free in the aquatic environment. Johnson (1975) observed no *C. shasta* infections in fish exposed to water maintained longer than 3 d in a sealed container. However, he suggested that static conditions in the containers may have caused a quicker death of *C. shasta* than normal.

DISTRIBUTION

The infective stage of *C. shasta* apparently emanates from the benthos of Lake Simtustus and is prevalent in the lower hypolimnion during the infective period. Because of the hypolimnic outlet, the epilimnion is permanent during the warm months, and the infective stage is unable to penetrate up through the thermocline. Hypolimnic water passes out of Lake Simtustus within 3 d, carrying infectious *C. shasta* down the Deschutes and Columbia rivers.

TABLE 4. Number of *Ceratomyxa shasta* infections observed after exposure of various numbers of susceptible rainbow trout to 94.6 L of Deschutes River water.

No. exposed	Trial 1[a]		Trial 2[b]	
	No. infected	(%)	No. infected	(%)
5	3	(60)	0	(0)
10	7	(70)	3	(30)
20	10	(50)	3	(15)
40	9	(23)	3-6-1[c]	(8)
80	10	(13)	4	(6)
160	11	(7)	4	(3)

[a]Trial 1 was conducted May 25–29, 1979, using Roaring River stock rainbow trout averaging 2.3 g.
[b]Trial 2 was conducted September 26–30, 1979, using Oak Springs (Diamond Lake) stock rainbow trout averaging 1.6 g.
[c]Three replicates were conducted using 40 fish per aquarium.

Distribution of infectious *C. shasta* in Lake Billy Chinook follows a pattern similar to Lake Simtustus (infective benthic waters), but affects a much smaller percentage of this reservoir. Because the Metolius River is considerably cooler during the summer than the Deschutes and Crooked rivers, it tends to fill the bottom of the reservoir, slowing the upward diffusion of benthic-associated waters. Infectious *C. shasta* reach the outlet and pass into Lake Simtustus only when thermal-induced mixing occurs in late summer or fall. However, the concentration of *C. shasta* is relatively low as a result of the large dilution factor, and also likely due to relatively low numbers of spores deposited in this section of the reservoir. Susceptible trout have not been released into Lake Billy Chinook within the past 10 yr (see Discussion — Abundance). In the upper portions of the Deschutes and Crooked River arms, the infective stage is present near the bottom as well as in the rivers entering these arms. Sanders et al. (1970) also showed these rivers to contain the infective stage. Because abundance experiments indicate a correlation between historical spore deposition and subsequent abundance of infectious *C. shasta*, the infective stage should be abundant in the upper portions of these two arms where spores from upstream sources would tend to settle.

The lack of infections in test fish exposed to the Metolius River and associated arm of Lake Billy Chinook is not fully understood. The infective stage was previously reported in the Metolius River in rainbow trout at Wizard Falls Trout Hatchery, but only after several months exposure time (J. E. Sanders, Oregon Department of Fish and Wildlife, Corvallis, OR, personal communication). It is apparent the Deschutes and Crooked rivers carry much higher concentrations of infectious *C. shasta* into Lake Billy Chinook than does the Metolius River.

Distribution and longevity studies suggest that under certain conditions reservoirs can interrupt the downstream movement of infectious *C. shasta* during most of the infective period. The reservoir must be sufficiently large and the outlet located far enough from the bottom so that water carrying infectious *C. shasta* from upstream sources or the benthos does not move to the outlet within 13 d. Round Butte Dam and Lake Billy Chinook meet both criteria. The outlet is located on a rock point of the flooded canyon wall and, when the

TABLE 5. Estimated abundance of the infectious stage of *Ceratomyxa shasta* in the lower Deschutes River at different times during 1979, 1980, and 1981.

Date sampled[a]	Test fish mean wt (g)	River temp. °C[b]	No. of infectious replicate 1−2−3 (mean)		*C. shasta*/m³
1979					
March 15	2.3	6.7	0−0−0	(0.0)	0
April 5	4.5	7.8	0−0−0	(0.0)	0
April 26	1.1	7.5	2−3−3	(2.7)	28
May 14	2.3	9.7	6−7−7	(6.7)	70
June 4	3.6	11.1	13−13−16	(14.0)	148
June 25	2.7	11.4	7−8−3	(6.0)	63
July 16	1.9	12.2	3−5−3	(4.0)	42
Aug. 6	2.5	13.1	3−11−7	(7.0)	74
Sept. 5	1.1	12.8	8−5−3	(5.3)	56
Sept. 26	1.6	12.8	3−6−1	(3.3)	35
Oct. 15	2.5	12.2	2−3−3	(2.7)	28
Nov. 5	3.6	11.7	2−2−2	(2.0)	21
Nov. 26	4.8	10.0	1−0−0	(0.3)	4
1980					
July 21	2.2	11.9	0−0	(0.0)	0
July 22	2.2	11.9	0−0	(0.0)	0
1981					
May 11	3.6	9.4	4−2−2	(3.3)	35
June 12	2.5	10.0	7−8−6	(7.0)	73
July 20	3.5	12.2	1−0−0	(0.3)	4
Aug. 16	4.6	12.7	0−0−0	(0.0)	0

[a]Test fish were exposed to Deschutes River water immediately after it was placed in aquaria.
[b]Mean river temperature during exposure. Temperature in aquaria varied approximately ±1°C depending upon air temperature.

reservoir is thermally stratified, draws water from relatively high in the hypolimnion.

TIMING

The beginning of the infective period varied from before March 31 to April 16−23 during the study. Initial infections were found progressively later each year, but this phenomenon may have been at least partially caused by the decrease in infectious units during the study period. Mean water temperatures when infections first occurred at the regulating dam site varied from 6.9°C in 1978 to 8.6°C in 1981. These temperatures are lower than those reported by Johnson (1979) and Schafer (1968). They implied that the water temperature must be 10°C before infections begin. In another study Weber and Knispel (1977) determined the infective period in the lower Nehalem River (Oregon) began between April 7 and 14 in 1976 when the mean water temperature was 7.8°C.

During timing studies, information was gathered on the relationships between exposure temperature, infection frequency, and mean time until death for the many groups of test fish used. Time until death was associated much more with infection frequency than with exposure temperature. Test groups which suffered very high infection frequencies (>90%) also had the shortest mean time until death (Fig. 3). Because high infection frequency is most likely caused by a large number of infectious units present, this condition must also lead to multiple infections of individuals, reducing the time until death. Conversely, in studies to determine the presence or absence of infectious *C. shasta*, if very low infection frequencies are to be detected, a long incubation period (100 d at 10°C) must be provided.

ABUNDANCE

When this study was initiated, the infective stage of *C. shasta* was very abundant in the hypolimnion of Lake Simtustus and downstream in the Deschutes River. High abundance has been demonstrated in other waters as well. Schafer (1968) found infections in all test fish exposed for only 2 h in Baum Lake (Sacramento River System, CA). Sanders et al. (1972) observed infections in juvenile coho salmon (*Oncorhynchus kisutch*) after exposure for only 30 min to Columbia River water at Bonneville hatchery.

In 1976, I hypothesized that infective-stage abundance in the Deschutes River was artificially high because of both the formation of Lake Simtustus (where spores could settle) and the tremendous production of spores resulting from infections of hatchery rainbow trout. About 90 000 highly susceptible rainbow trout (length >15 cm) were liberated annually into Lake Simtustus until 1977 (7300 liberated), when managing agencies terminated this practice. The bioassay technique allowed for quantification and monitoring of abundance levels after termination of trout releases. Abundance was still high during 1978, but then declined substantially at least through 1980. Because termination of trout releases was the only management practice altered, evidence indicates a direct relationship between numbers of spores deposited and subsequent numbers of infectious *C. shasta*.

The bioassay technique for estimating abundance of infec-

tious *C. shasta* is valid if the following two assumptions are true: (1) All infectious *C. shasta* present in test aquaria enter test fish and initiate infections; and (2) one infectious *C. shasta* can cause clinical infection and death of one susceptible fingerling trout. Evidence for the first assumption was seen when test fish exposed to the same water subsequent to initial exposures suffered no infections (see Results — Longevity). However, whether all infectious *C. shasta* actually entered the first test fish or if the presence of these test fish deactivated the remaining *C. shasta* is not known. Further proof for this assumption must await additional knowledge of the infective stage. Evidence for the second assumption was seen when a similar number of infections developed per aquarium, even when large numbers of test fish were exposed (see Results — Abundance). Johnson (1975) found that the interperitoneal injection of one *C. shasta* trophozoite (vegetative stage) into a healthy fingerling cutthroat trout (*Salmo clarki*) also would lead to ceratomyxosis and death.

The bioassay technique is subject to the following possible sources of error: (1) if numbers of infectious *C. shasta* are high in relation to the numbers of test fish used, multiple infections of individual fish are likely, leading to underestimation of *C. shasta* numbers; (2) some test fish could be resistant enough to withstand infection by one *C. shasta*. Chances of infections not manifesting themselves likely increase as larger test fish are used; (3) actual death may be caused by secondary bacterial infections prior to *C. shasta* spore formation. From my observations, *C. shasta* spores are more likely observed when test fish are held during the incubation period at 10°C rather than at warmer temperatures.

Contributions to the Life History of *C. shasta*

In a normal host–parasite relationship, long-term survival of the parasite is dependent upon a long-term association with its host (Dineen 1963). But this seemingly presents a problem with *C. shasta*. Because it is a tissue parasite invading vital organs (Johnson 1975), infections in juveniles culminating in spore formation are normally fatal (Zinn et al. 1977). A factor causing mortality in an animal population promotes genetically transferred resistance against that factor in the remaining population which reproduces successfully. Genetic resistance to ceratomyxosis has been demonstrated in stocks of fall-migrating chinook salmon (*O. tshawytscha*) from river systems where *C. shasta* is found (Zinn et al. 1977), as well as in native Deschutes River rainbow trout (Johnson 1975).

The success of *C. shasta* appears linked with its ability to infect adult salmonids nearing maturity. Infections in spawning adult Pacific salmon are quite common (Wood and Wallis 1954; Sanders et al. 1970; Coley 1978) even though these same fish were apparently resistant as juveniles. Progress of these infections is likely facilitated through failure of the maturing salmon's immune system and the natural atropism of his digestive system, the major area of infection. Alternatively, some destruction of digestive organ tissue by *C. shasta* at this time in the salmon's life is not necessarily detrimental to its remaining longevity. Thus, a normal host–parasite relationship can be maintained.

Adult spring-migrating chinook salmon ascend the Deschutes River beginning in April with peak numbers appearing between May 15 and June 15. This timing coincides with peak concentrations of infectious *C. shasta* measured during this study. These fish ascend to headwater areas where they mature during the summer and spawn in late August and September. The relatively long prespawning freshwater residence allows for *C. shasta* to progress to the spore stage prior to the host's spawning and natural death. Spores are released in headwaters during the major low-flow period of the year and have maximum opportunity to settle-out downstream. Moser (1977) determined that, because of their shape, spores of the genus *Ceratomyxa* are relatively slow to settle as compared to spores of other myxosporeans. Several authors (Schafer 1968; Wood 1974) have associated formation of the infective stage with waters of low velocity, and it seems probable that this requirement is linked to the settling rate of these spores.

It was historically hypothesized that polar filaments serve to anchor myxosporean spores to the host fish's gut wall during the infection process (Erdman 1917; Kudo 1930). I propose that with *C. shasta*, at or soon after settling, unknown processes lead to the firing of polar filaments which function to anchor the spore to the river substrate during a required interval prior to infective stage emergence (at least over one winter). A mechanism to attach the spore would seem necessary in many river systems to prevent floods from flushing the spores to the ocean. During the required interval or "aging period," unknown forces influence the spore, ultimately leading to the emergence of an infective stage. This aquatic stage (as yet undescribed) must encounter and infect a new host within ~10 d or perish.

Changes that happen and environmental criteria required between spore deposition and infective stage emergence are unknown. An "aging period" of several months in the presence of mud has been determined necessary for the production of infectious *Myxosoma cerebralis*, the whirling disease myxosporean (Hoffman and Putz 1969; Taylor and Lott 1978). However, environmental requirements appear even more stringent for *C. shasta* as spores are carried by adult anadromous salmonids into many waters where the infective stage has never been demonstrated (Johnson et al. 1979; Sanders et al. 1970). Alternate host(s) or an "activator species" might be required during this interval. However, it is doubtful that alternate-host distribution is the determining factor in *C. shasta* infective stage distribution due to the diverse habitats (high lakes to low-level coastal streams; Johnson et al. 1979) where the infective stage is produced. Factors involved in the spore to infective stage transformation might be physical and chemical as well as biological. A first step in determining these factors would be comparison of physical, chemical, and biological parameters of source areas with like parameters of areas where spores are known to settle, but the infective stage is not produced.

The determination that spore numbers influence subsequent infective stage numbers suggests potential resource consequences of environmental alterations. In addition to the construction of reservoirs (enhancing settling of spores) and introductions of susceptible host fish (artificially increasing spore production), factors which reduce spore mortality might be important determinants of subsequent infectivity and host fish mortality. Upstream storage reservoirs which serve to

reduce flood peaks and capture silt would likely reduce spore mortality from scouring and inundation. With increased numbers of infectious *C. shasta*, potential host fish, resistant to previous exposure levels, would suffer increased infection, further increasing spore production and infectivity. Juvenile anadromous salmonids, not seriously infected normally, could succumb, as found in previous studies on the Deschutes River (Ratliff 1981). Results of *C. shasta* timing studies (this paper) indicate that delay of spring smolt emigration by the presence of reservoirs (Raymond 1979) also greatly increases exposure intensity. However, juvenile mortality would be masked by predation and/or occur in the ocean after emigration. Thus, serious *C. shasta*-induced losses in salmonid populations probably occur as an ecological consequence of environmental alterations, yet go largely unnoticed.

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Population Dynamics of an Estuarine-Dependent Fish, the Spot (*Leiostomus xanthurus*), Along a Tidal Creek–Seagrass Meadow Coenocline[1]

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WEINSTEIN, M. P. 1983. Population dynamics of an estuarine-dependent fish, the spot (*Leiostomus xanthurus*), along a tidal creek–seagrass meadow coenocline. Can. J. Fish. Aquat. Sci. 40: 1633–1638.

To study the population dynamics of young-of-the-year spot (*Leiostomus xanthurus*) I released 6981 marked fish midway up the tidal creek portion of a small (<20 ha) marsh creek–seagrass meadow coenocline. Holding mortality experiments (96 h) indicated that 61.5%, or 4300 individuals, survived the marking process to constitute the population available for recapture. Over a 90-d study period, 212 marked fishes were recaptured. From plots of the ratio of marked to unmarked individuals in subsequent samples, I concluded that the population was resident in the creek for up to 182 d with the average individual present for 91 d. When this population turnover rate was compared to the total population decay rate (marked plus unmarked fish), the exchange between habitats (immigration/emigration) accounted for about 26% of the total decay rate, with the remainder attributed to natural mortality. By correcting the overall disappearance rate for population turnover due to immigration/emigration, and using this adjusted value as a measure of instantaneous mortality (Z), the estimated production in this population was 21.8 kcal (91342 J)·m^{-2}·d^{-1}. This figure is over six times greater than previously reported values for this species for all size classes over the entire growing season.

WEINSTEIN, M. P. 1983. Population dynamics of an estuarine-dependent fish, the spot (*Leiostomus xanthurus*), along a tidal creek–seagrass meadow coenocline. Can. J. Fish. Aquat. Sci. 40: 1633–1638.

Dans le but d'étudier la dynamique des populations de tambours croca (*Leiostomus xanthurus*) de l'année, 6 981 poissons ont été mis en liberté à mi-chemin de la portion soumise à l'action de la marée d'un barachois marécageux formant coenocline de faible étendue (<20 ha) avec une prairie de persil d'eau. Des expériences de mortalité en stabulation (96 h) indiquent que 61,5 % ou 4 300 sujets survivent au marquage et constituent la population accessible à la recapture. Sur une période de 90 jours, 212 poissons marqués sont recapturés. Les tracés du ratio individus marqués/non marqués dans des échantillons subséquents me permettent de conclure que la population est demeurée dans la barachois jusqu'à 182 jours, la moyenne individuelle étant de 91 jours. Une comparaison de ce taux de renouvellement de la population avec le taux de désintégration de la population totale (poissons marqués plus poissons non marqués) indique que l'échange entre habitats (immigration/émigration) explique environ 26 % du taux de désintégration total, la balance étant attribuée à la mortalité naturelle. En corrigeant le taux global de disparition pour tenir compte du renouvellement de population dû au quotient immigration/émigration et utilisant cette nouvelle valeur comme mesure de la mortalité instantanée (Z), la production de cette population est estimée à 21,8 kcal (9 1342 J)·m^{-2}·d^{-1}. Ce chiffre est six foix supérieur aux valeurs signalées antérieurement pour cette espèce, de toutes tailles et pour toute la saison de croissance.

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SPOT (*Leiostomus xanthurus*) is seasonally abundant in coastal waters from Delaware Bay south through the Gulf of Mexico. Adults spawn offshore during fall and winter and the young recruit to estuaries in late winter and early spring.

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Within estuaries, juveniles rapidly become epibenthic and accumulate in shallow tidal marshes and seagrass meadows (Herke 1971; Weinstein 1979; Bozeman and Dean 1980; Weinstein et al. 1980a, b). Similar life history patterns occur in many other fall and winter spawning species along the Atlantic coast, including menhaden (*Brevoortia* spp.), flounders (*Paralichthys* spp.), Atlantic croaker (*Micropogonias undulatus*), and pinfish (*Lagodon rhomboides*) (Weinstein 1981). However, different taxa may prefer or select different habitats, several species are more abundant in deep water compared to the shallows (e.g. Weinstin et al. 1980b; Weinstein 1982), and maximum densities are often associated with narrow salinity ranges (Gunter 1961; Copeland and Bechtel 1974; Weinstein et al. 1980a). Recent evidence (Polgar 1982) also attributes some distribution patterns to differential mortality due to size-selective predation.

It is not yet possible to determine the role of physiological constraints, resource availability, predation refugia, or various interactions in habitat selection. Moreover, general population dynamics for all of the taxa described above are poorly understood. Because these populations are generally regarded as open systems, it has been exceeding difficult to apply standard population models (Seber 1973). Developing such models remains a fundamental need in estuarine finfish research.

Here, I use mark–recapture information to describe population dynamics of young-of-year spot in a contiguous tidal creek/seagrass meadow ecosystem. My objectives were to (a) determine residence time and extent of movement between the creek and grassbed; (b) measure the turnover rate of spot in the creek; (c) determine if spot prefer one habitat type over another; (d) estimate the mean growth rate of spot in the creek, and (e) during their period of residency, estimate spot production in the creek.

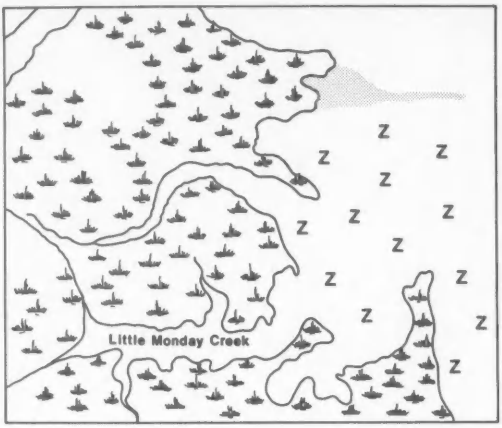

FIG. 1. Tidal creek–seagrass meadow study area. Seagrass meadow dominated by *Zostera marina* (Z). Shaded area indicates location of sandbar.

TABLE 1. Survival rates of marked spot (*Leiostomus xanthurus*), held for 96 h in 600-L tanks of running seawater

	Number alive at end of:					Survival rate	
	0 h	24 h	48 h	72 h	96 h	N	%
Tank 1	88	80	65	62	59	59	67.0
Tank 2	82	75	57	49	46	46	56.1
						Mean survival:	61.6

Materials and Methods

The study area was Little Monday Creek in the Guinea Marsh system of the York River estuary, Virginia (Fig. 1), a relatively small polyhaline tidal creek (<4 ha) which terminates in a patchy (65% cover) mixed grassbed consisting of *Zostera marina* and *Ruppia maritima* (R. J. Orth, Virginia Institute of Marine Science, Gloucester Point, VA 23062, USA, personal communication). The grassbed (~16 ha) being well defined (Fig. 1) and partially enclosed by shoreline and sandbars provided an opportunity to examine environmental grain, and determine from returns of marked fish if spot moved freely through the marsh–seagrass continuum or selected a particular portion of it (i.e. whether spot perceived this coenocline as "coarse" grained or "fine" grained (Levins 1968)). Length of residency in each habitat also could be determined, and by sampling individuals leaving the area, population turnover rate could be partitioned into emigration and natural mortality.

Because estuarine species usually have a high turnover rate due to mortality and emigration, large numbers of fish had to be marked. To meet this criterion, "sandblasting" with fluorescent pigments was used (Jackson 1959; Phinney et al. 1967; Arnoldi et al. 1976; Engelhardt 1977). Fish were captured with a 30.5-m bag seine (6.5-mm mesh), held temporarily in large containers, and then released in the area of capture immediately after being marked. Compressed air from SCUBA tanks at 6.5 kg·cm,$^{-2}$ pressure was used to batch-spray about 30 fish at a time (Tohiyat 1979; Dolloff and Huish 1980). On June 7 and 8, 3138 fish marked with red pigment were released in the upper tributaries of Little Monday Creek; on June 9 and 10, 3843 fish marked with green pigment were released about midway up the main portion of the creek. The total number of fish released was 6981.

To determine what rate of mortality might be expected for marked fish, I retained six randomly selected batches totaling 170 individuals. These fish, divided into two groups of 82 and 88, respectively, were held at the laboratory in two 600-L circular tanks filled with running seawater. At the end of 96 h (Table 1), 67% of one group and 56.1% of the other (mean 61.6%) had survived. Therefore, it was concluded that 4300 of the marked fish had survived for at least 4 d. As all of the 170 fish had been well marked with pigment, I assumed that all of the released fish also had been well marked.

Sampling to recapture marked fishes began on June 14. The creek was sampled on 13 subsequent dates through September 10. Until July 6 it was sampled about every 4 d. After that, the intervals were once a week (until August 4) or twice a week (after August 4). Additional samples were collected by otter trawl in the adjacent grassbed during the period June 4

TABLE 2. Recapture data for spot (*Leiostomus xanthurus*) in Little Monday Creek. t_{cum} = cumulative number of days between samples. n_i = number of individuals in the ith sample. m_i = number marked in the ith sample. CPUE = catch-per-unit-effort.

Date	t_{cum}	Number caught (n_i)	Number marked (m_i)	Ratio (m_i/n_i)	CPUE (n/m^2)
June 14	0	3121	75	0.0240	4.98
June 18	4	2046	27	0.0132	4.89
June 22	8	1131	28	0.0248	1.80
June 25	11	911	12	0.0132	1.45
July 2	18	1804	25	0.0139	2.16
July 6	22	678	5	0.0074	0.81
July 15	31	918	6	0.0065	0.63
July 21	39	1029	15	0.0146	0.82
July 28	46	697	7	0.0100	0.48
Aug. 4	53	425	4	0.0094	0.23
Aug. 23	72	663	3	0.0045	0.11[a]
Sept. 5	85	262	2	0.0076	0.028[a]
Sept. 10	90	245	1	0.0041	0.039[a]
Totals		13930	210		

[a]Trawl catch, all other collected with 30.5-m bag seine.

TABLE 3. Estimated growth rates for spot (*Leiostomus xanthurus*) based on recaptures of marked fish.[b]

	Mean length (mm)	n	ΔL	Δt	$G(\Delta L/\Delta t)$
Holding experiments (June 10–14)	48.6	70			
June 18	51.7	27	3.1	6	0.52
July 2	58.0	24	6.3	14	0.45
July 15	64.7	6	6.7	13	0.52
July 21	67.1	15	2.4	6	0.40
July 28	71.7	7	4.6	7	0.66
Aug. 4	79.8	4	8.1	7	1.16
Aug. 23	86.2	4	6.4	19	0.34
Sept. 7.5[a]	96.0	3	9.8	15.5	0.63

[a]Mean values for September 5 and 10, only three marked fish were captured on these two dates.
[b]n = number of individuals, ΔL = change in length, Δt = time interval, G = growth.

through July 28. At least two hauls were made using the 30.5-bag seine at permanently established stations in the upper tributaries, in mid-creek, and near the creek mouth. In addition, single 2- to 3-min hauls of a 4.9-m semiballoon otter trawl with wings and body of 19-mm mesh and a liner of 6.5-mm mesh were made at a uniformly placed array of six stations in the seagrass meadow just outside of the creek.

Because pigments on recaptured fishes were not visible under field conditions, it was necessary to return all fish to the laboratory for examination under long wavelength ultraviolet illumination. Marked individuals were routinely measured for standard length, although this was not done on all sampling dates.

Total decay rate (mortality + emigration) in the tidal creek spot population was expressed by regressing $\log_{10}$ catch-per-unit-effort (CPUE) on sampling date. The regression of $\log_{10}$ marked/unmarked (m_i/n_i) individuals on sampling date was used to indicate population turnover rate in the creek. This ratio is similar to that of Parker (1955) where recruitment to a bluegill (*Lepomis macrochirus*) population was examined. In the present instance, however, I was tracking changes in both the numerator (marked fish leaving the population) and denominator (unmarked fish moving into Little Monday Creek from adjacent areas), rather than the denominator alone (= recruitment, Parker 1955).

Secondary production (P) was calculated by a computer version of the basic production model (Ricker 1946; Allen 1950), as modified by Adams (1976) where:

$$(1)\quad P = G\bar{B}$$

$$(2)\quad G = \log_e \bar{w}_2 - \log_e \bar{w}_1/\Delta t$$

$$(3)\quad \bar{B} = B_0(e^{G-Z} - 1)/G - Z$$

$$(4)\quad Z = -(\log_e N_2 - \log_e N_1/t.$$

G is the instantaneous growth rate; $\bar{B}$ is the mean standing stock biomass in a given time interval; Z is the instantaneous mortality rate; $\bar{w}_1$ and $\bar{w}_2$ are the mean weights of individuals at each station at time t_1 and t_2, respectively, and N_1 and N_2 are the number of individuals/m^2 present at t_1 and t_2, respectively.

To estimate biomass, standard length (SL) was converted to dry weight using the relationship: $\log_e (w) = 3.2726 \log_e SL - 5.8751$ ($r^2 = 0.999$; Brooks et al. unpublished results).

A conversion value of 5.139 kcal (21532 J)·g^{-1} (dry weight) for spot was used (Thayer et al. 1973). The instantaneous mortality rate Z was adjusted to reflect the difference between the slopes of the CPUE and m_i/n_i curves; i.e. the partitioning of the total decay rate into mortality and population turnover rate. CPUE was also adjusted to reflect gear efficiency by using a value of 40.6% determined for the 30.5-m seine on juvenile white perch (*Morone americana*) and striped bass (*M. saxatalis*) (Texas Instruments 1978). It was assumed that similar-sized spot would be equally susceptible to this gear (see also Weinstein and Davis 1980).

Results and Discussion

Because the spot population in Little Monday Creek was expected to be open, it was not immediately certain what patterns the returns of marked fishes might follow. Hence, my approach was to track a single cohort, i.e. the marked population, by intensive sampling in time and space. If the general assumptions of the marking program, other than the assumption of negligible emigration were met, there would be at least three expected outcomes of this effort (Seber 1973):

Case 1. Most returns would come from Little Monday Creek, indicating that spot continued to reside in the tidal creek.

Case 2. After a "short" interval, returns would be collected uniformly throughout the area (creek and grassbed) and immediately outside of the site.

Case 3. After a "short" interval the number of returns would be drastically low, indicating that the population was turning over rapidly due to a combination of immigration and/or emigration. If rapid turnover occurred, it most likely would be due to a rough balance between the two processes (it was safely assumed that recruitment would not be a problem, as few spot arrived in the Chesapeake Bay after early May).

Mortality, of course, would be superimposed onto any of these patterns, and although it was possible that a combination of the above might occur, e.g. Case 2 grading into Case 3 (over a longer time interval), other possibilities were judged trivial, or were expected to have a low likelihood of occurrence.

Returns of marked fish indicated that most spot remained in Little Monday Creek and that few ventured into the adjacent grassbed. Only 2 of 2310 (0.087%) fish caught in the grassbed were marked, whereas 210 of 13 930 (1.5%) caught in the creek were marked. The 17× higher return rate from Little Monday Creek was an early indication that considerable residency was taking place in this area.

Standing crop in the creek was estimated by two different methods, one based on the number of fish caught/m^2 and the other on the ratio of unmarked to marked fish. Each seine haul covered 523 m^2. On June 14, and 18, the mean catch per haul was 2584, or 4.94/m^2. Because the creek area was about 4 ha, the total number of spot in the creek at the beginning of the experiment was estimated to be 197 600 (40 000 × 4.94). The estimate based on the ratio of marked to unmarked fish, $N = (C/R)M$ (Ricker 1975), was 217 825, where N = number of fish in the population, C = number of fish in the sample, M = the number of marked fish in the population, and

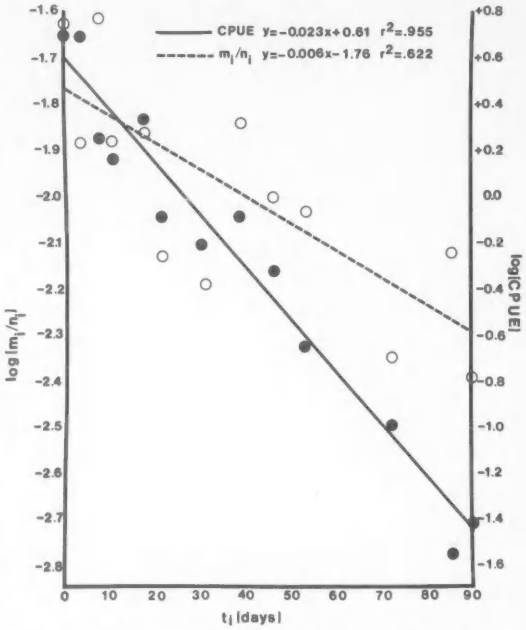

FIG. 2. Results of marking study at Little Monday Creek (Guinea Marsh system). Log_{10} of catch-per-unit-effort ($\log_{10}$ CPUE) is plotted against the cumulative number of days (t_i) between samples. Similarly, $\log_{10}$ of the ratio of marked to unmarked fish ($\log_{10} m_i/n_i$) in each sample is plotted against t_i. Closed circles, CPUE; open circles, m_i/n_i.

R = the number of marked fish in the sample. These independent estimates agree within 10.2% indicating that my estimate of surviving fish is likely correct and by the start of the recapture period, marked individuals were randomly dispersed throughout the population.

Total decay rate (mortality plus emigration) of the spot population in the tidal creek, along with the ratio of marked to unmarked (m_i/n_i) individuals in each sample is shown in Table 2 and Fig. 2. The slope of the equation of the CPUE line (Fig. 2), $y = 0.023x + 0.611$, was significantly different from zero ($P < 0.01$; $r^2 = 0.955$), as was the slope of the regression of m_i/n_i on sampling date, $y = 0.006x - 1.76$ ($P < 0.01$; $r^2 = 0.622$). Furthermore, comparison of the slopes of log CPUE and $\log_{10}$ (m_i/n_i) regressions differed significantly ($t = 8.095$, $P < 0.01$).

It is clear that exchange of spot between habitats is a considerably slower process than might have been expected. Population turnover rate was about 182 d, with an average individual remaining in the creek for 91 d (Fig. 2). These residency estimates reflect rates calculated for the 90-d study period. In actuality a rapid increase in emigration rate would be expected with the onset of seasonally cold weather, usually in early November in the Chesapeake Bay (Markle 1976; Chao and Musick 1977). The exchange rate also seemed to be localized among marsh creeks (only two marked individuals

were recaptured over the grassbed) and involved, at most, a very gradual rate of emigration (Case 3 above). These observations confirmed previous studies based on abundance and length–frequency distributions, which conjectured the rate of emigration (prior to fall mass exodus) to be relatively low with a substantial period of residency exhibited by individual spot (Herke 1971; Parker 1971; Weinstein and Walters 1981). It is important to point out that this study entailed a creek system of only 4 ha. Considered on a larger scale (for example, the Guinea Marsh system comprising several hundred hectares with associated tidal creeks), it is likely that the recruited population is largely resident for the entire growing season.

Biomass production of spot between June 12 and September 10 was estimated to have been 0.382 $g \cdot m^{-2}$, or 1960 cal (8212 J)$\cdot m^{-2}$. In calculating these figures, I assumed that population turnover rate was about 26% of the total decay rate (Fig. 2) and that growth for all fish reflected the increase in length of marked fish (Table 3). Values of N were adjusted to reflect emigration of marked fish.

Weinstein and Walters (1981) reported a mean value of 257 cal (1077 J)$\cdot m^{-2}$ for spot production in four marsh systems of the Cape Fear River estuary, North Carolina. This figure was based on an expected residency of up to 7 mo but was not corrected for gear efficiency or emigration. Similarly, Adams (1976) production estimates of 37 (155 J) and 356 (1492 J) cal$\cdot m^{-2}$ for all age groups of spot in seagrass meadows at Bogue Sound and Phillips Island, North Carolina, respectively, also probably represent significant underestimates of actual production. In addition, our recent studies (Weinstein and Brooks 1983) indicate that spot may be transient in grassbeds, not residents. Production estimates for spot in the seagrass meadow, therefore, may not accurately reflect the role of this habitat, but may largely reflect energy transfers that are occurring elsewhere.

Spot apparently perceive Little Monday Creek and adjacent grassbed as a coarse-grained environment (Levins 1968) and tended to remain in the marsh creek, rather than moving freely along the marsh–seagrass coenocline. These results confirm observations of Weinstein and Brooks (1983) in a much larger (>500 ha) marsh–seagrass system where, throughout the year, spot were nearly 4× more abundant in the tidal creek compared to the nearby grassbed. However, spot were larger in this creek earlier in the season, which suggests that larger individuals in the population are most likely to emigrate.

The high degree of residency exhibited by spot recruited into the area in a more or less random fashion (from spawn originating offshore) indicates that active habitat selection is taking place. The procedures developed in this paper should prove valuable for measuring aspects of population dynamics of open populations of estuarine species, an area which has received little consideration. One obvious direction for future research would involve the adaptive values associated with habitat choice. Becaue of commonalities in general life history strategies, it is also possible that the spot shares similar traits with other estuarine-dependent species.

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Substrate Selection by Tubificid Oligochaetes

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Groups composed of *Tubifex tubifex* and *Limnodrilus hoffmeisteri* collected from Keating Channel and Hanlan's Point in Toronto Harbor, Lake Ontario, preferred Keating Channel sediment over Hanlan's Point sediment in laboratory substrate selection experiments. The degree of preference did not differ between the two species. Substrate selection appears to be a taxic response to dispersing microbiota or molecules with molecular weight greater than 12 000–14 000. Percent organic content, concentrations of selected chemical elements and particle size do not account for the observed preference. However, there was a significant correlation between the abundance of heterotrophic aerobic bacteria in sediment and tubificid preference. We suggest that the microbial constituents of the sediment are more important than its physical and chemical properties in influencing substrate selection by tubificids.

McMurtry, M. J., D. J. Rapport, and K. E. Chua. 1983. Substrate selection by tubificid oligochaetes. Can. J. Fish. Aquat. Sci. 40: 1639–1646.

Dans des expériences de sélection du substrat en laboratoire, des groupes formés de *Tubifex tubifex* et *Limnodrilus hoffmeisteri* recueillis dans le chenal Keating et à la pointe Hanlan's, dans le port de Toronto, dans le lac Ontario, montrent une préférence pour le sédiment du chenal Keating par rapport à celui de la pointe Hanlan's. Le degré de préférence ne diffère pas chez les deux espèces. La sélection du substrat semble être une taxie en réponse à des microbiocénoses se dispersant ou à des molécules de poids moléculaires supérieurs à 12 000–14 000. La teneur en matière organique, les concentrations d'éléments chimiques choisis et la taille des particules n'expliquent pas cette préférence. Cependant, il y a corrélation significative entre l'abondance des bactéries aérobies hétérotrophes dans le sédiment et la préférence des tubificides. Nous croyons que les constituants microbiens du sédiment sont plus importants que ses propriétés physiques et chimiques dans la sélection du substrat par les tubificides.

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In nature, animals usually do not occupy the full range of environmental conditions under which they can survive (Elton 1927). Optimal habitat is selected by continually assessing and responding to information received from the environment (Meadows and Campbell 1972). The ultimate benefits of this behavior are increased survival and reproductive success. When the accessible habitat is heterogenous, habitat selection can be important even to animals of low mobility, such as the tubificid oligochaetes.

Many environmental variables including water temperature, oxygen concentration, presence of competitors or predators, and substrate properties could influence habitat selection by tubificids. Studies of the influence of substrate properties on habitat selection by tubificids have produced conflicting results. Wachs (1967) found that *Tubifex tubifex* preferred nutrient-rich sediment (i.e. high in organic C and total N) regardless of particle size while Zahner (1967) found that this species chose coarse-grained nutrient-poor sediment (i.e. low in organic C, organic N, and organic P) over fine-grained nutrient-rich sediment. The importance of bacteria in the diet of tubificids is now well established (Brinkhurst and Chua 1969; Wavre and Brinkhurst 1971; Brinkhurst et al. 1972). Further, Coler et al. (1967) have shown that mixed populations of tubificids can discriminate between different species of bacteria. The role of sediment bacteria in habitat selection has not yet been directly considered, though

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FIG. 1. Toronto Harbor showing Keating Channel (1) and Hanlan's Point (2) sampling sites. Harbor currents indicated by arrows.

Brinkhurst's (1974) observations of sediment discrimination by tubificids after additions of tubificid fecal material hint at the importance of bacteria.

The purpose of this paper is to investigate substrate selection by tubificids and identify the dominant substrate properties that influence it. We assume that while tubificids can respond to many different environmental characteristics, the relative importance of these differs and only a few of them exert primary influence on the preference response in the natural environment (Cummins and Lauff 1969).

The tubificid population of Toronto Harbor, Lake Ontario, was chosen for study because it is distributed over a gradient of organic pollution (Brinkhurst 1970). Diversity is lower and abundance higher in the Keating Channel area (which receives sewage effluent from the Don River) than in the Hanlan's Point area on the opposite side of the harbor (Fig. 1). The specific questions addressed were: (1) Do mixed species groups of worms have a preference for Keating Channel (KC) sediment or Hanlan's Point (HP) sediment in laboratory selection experiments? (2) Does preference depend on preadaptation to a specific habitat? (3) How does substrate selection by individual worms compare with substrate selection by groups? (4) Is substrate selection a taxis (movement directed towards or away from the source of stimulation) or a kinesis (variation in amount of locomotory activity which is not oriented to the direction of the stimulus) (Fraenkel and Gunn 1961)? (5) What influence do the physical, chemical, and biological properties of sediment have on substrate selection? In particular, does bacterial abundance influence preference?

Methods

Substrate Selection by Groups

Worms and sediment were collected during the summers of 1979 and 1980 from Toronto Harbour at Hanlan's Point (HP) and Keating Channel (KC) (sampling sites shown on Fig. 1) using an Ekman dredge. Sediment containing worms was brought to the laboratory, covered with aerated dechlorinated tapwater and held at 14°C in a temperature controlled room. Additional sediments from both locations and sand from the Hanlan's Point beach were collected at the same time and sieved in the field with a number 30 USA series wash bucket (600 μm pore size) to remove macrofauna. The sieved sediments and sand were also brought to the laboratory, covered with aerated dechlorinated tapwater and held at 14°C.

Brinkhurst (1970) reported the dominant tubificids in Toronto Harbour to be *Tubifex tubifex* (Müller), *Limnodrilus hoffmeisteri* Claparède and *Peloscolex multisetosus* (Smith) (renamed *Quistadrilus multisetosus* by Brinkhurst, 1981). As *Quistadrilus* was not abundant in our sediment samples, substrate selection experiments were done using only the first two species. Species proportions were maintained similar to field proportions. Worms were separated from sediment using a number 30 sieve and washed into a white enamel tray. They were then sorted with a Pasteur pipette and identified under a stereo microscope using the methods of Brinkhurst (1965 and 1968). With this method, up to six percent of worms identified as *L. hoffmeisteri* could be other *Limnodrilus* species (Brinkhurst 1970).

Four plastic perforated cups (15 cm high, 5.6 cm inside diameter, 0.5 cm perforations placed 2 cm apart over the bottom 9 cm of the cup) were fitted inside with removable plastic sleeves and filled to the 5 cm mark with the substrate to be offered for choice. Two of the cups were filled with sieved HP sediment and the other two with sieved KC sediment. The cups were filled by extruding the sediment from a plastic bag with one corner cut off. One cup was placed in each quadrant of a plastic tank (29 cm diameter, 29.5 cm height) with similar treatments occupying opposite quadrants and sieved HP sand was packed around the cups until it was even with the level of the substrate inside the cups. Dechlorinated tapwater was added to the tank until it covered the tops of the cups. Aeration of the water maintained oxygen near 100% saturation and the temperature was held at 14°C. Five experiments were done during the summers of 1979 and 1980 with two tanks per experiment. Three hundred worms were added to the center of the tank on the sand and the collars removed from the cups to begin the experiment. In the first three experiments, worms were from Keating Channel; in experiments 4 and 5 they were from Hanlan's Point. Tanks were exposed to overhead lights during the day, but it is unlikely that this disturbed worm behavior, since in later experiments with individual worms in which aquaria were not exposed to light, similar results were observed. Tanks were rotated on the bench to avoid favoring any one treatment.

Worm activity was observed daily, noting burrowing and accumulation of feces. After 8 d, the plastic collars were reinserted, water was siphoned off and the sediment in each cup sieved separately with a number 30 sieve. The worms retained were counted and identified.

The numbers of worms in each sediment type were summed for each tank to reduce within-treatment variability and to simplify presentation of the data. The procedures used for *G*-tests of independence and goodness-of-fit and calculations of exact probability are from Sokal and Rohlf (1969).

Substrate Selection by Individuals

A more restrictive experimental setting than that described

above was required to observe the movement of individual worms. Two plastic nonperforated cups (dimensions as above) were connected at the 5 cm mark by means of a 14 cm length of 2.5 cm diameter transparent Tygon tubing and placed in a small aquarium. The tubing had been half-filled with HP sand and an opening at the top allowed introduction of worms by Pasteur pipette. The cups were then filled with sieved sediment (KC sediment in one, HP sediment in the other) to a level even with the sand in the tubing. Dechlorinated tapwater was added to the aquarium until it covered the tops of the cups. The sand in the tubing was smoothed out when the aquarium was full. After allowing the sediment in the aquarium to settle for 0.5 h, a single *T. tubifex* from Keating Channel was placed on the sand in the center of the tube and its movement watched until it entered one of the cups. This experiment was conducted with *T. tubifex* only as the trials are very time consuming. Ten aquaria were run simultaneously.

When all 10 worms had entered cups an air stone was placed in the center of each tank, overhead lights extinguished and the tanks left for 2 d. Water temperature was maintained at 14°C. After 2 d, sediment from both cups in each tank was sieved to determine the location of the worm. Fresh sediment was used for subsequent runs.

The *G*-test for goodness-of-fit with Yates' correction factor was applied to the proportion of total worms choosing each substrate.

Sediment Characteristics

Organic content, element analysis, and particle size — Percent organic content of KC and HP sediment samples was determined by loss on ignition. Samples were obtained from sieved sediment stocks used in substrate selection experiments. The samples were dried at 65°C for 12 h and ignited in a muffle furnace at 550°C for 3 h.

KC and HP sediments were analyzed for concentrations of the total phosphorus, nitrate nitrogen, sodium, copper, lead, zinc, manganese, iron, nickel, cobalt and cadmium. Samples for total phosphorus, nitrate nitrogen, and sodium analysis were taken from sieved sediment stocks used in substrate selection experiments. Samples for analysis of the remaining metals were taken using a Ponar grab. A subsample of each grab, taken with a plastic cylinder, was sieved with a stainless steel number 30 sieve, allowed to settle, and frozen until final preparation for atomic absorption spectrophotometry. The ascorbic acid method (American Public Health Association 1971) was used for total phosphorus. The samples were digested in 5 mol L^{-1} H_2SO_4 and ammonium persulphate. The brucine method (APHA 1971) was used for nitrate nitrogen except that there was no addition of sodium arsenite or sodium chloride. Concentrations of both elements were determined by flame absorption spectrophotometry with deuterium background correction.

Sediment to be analyzed for metals other than sodium was prepared by drying at 65°C, digesting overnight in nitric and hydrochloric acids, and filtering through glass fibre filters. The filtrate was then analyzed by flame absorption spectrophotometry. Samples for sodium analysis were dried as above and ignited at 550°C for 3 h to combust the organic matter. The organic-free sediment was held in 2% HCl for 1 d and then analyzed by flame atomic absorption spectrophotometry.

Four 50-mL samples taken from sieved sediment stocks were dried overnight at 60°C; 20–30 g of each of these samples were analyzed by the hydrometer method which gave a distribution of particles less than 36 μm in diameter. The procedure used was that of Day (1965). Distribution of particles from 63 to 600 μm in diameter was obtained by wet sieving the samples used in the hydrometer analysis. The fractions retained by 500, 250, 125, and 63 μm pore size brass sieves were dried at 95°C and weighed. The fraction of sediment in the 36–63 μm range was obtained by subtraction.

Estimates of bacterial abundance — Estimates of the abundance of heterotrophic aerobic bacteria in KC and HP sediments were made by culturing diluted sediment on tryptic soy agar plates and counting the number of colony-forming units (CFU) after incubation (APHA 1971). Samples were obtained from sediment stocks collected May 26 and 27, 1980. The correct dilution factor was obtained through much trial and error and was in this case 1:80 000 for KC sediment and 1:4 000 and 1:10 000 for HP sediment. Four plates were prepared for each dilution; 1 mL of the diluted solution was spread on each agar plate. Plates were inverted after 0.5 h to prevent condensation from interfering with bacterial growth and incubated at 20°C for 30–40 h.

Even after trying a variety of dilutions, not more than two countable plates were obtained at any one dilution. Spreading bacteria obscured other colonies and bacteria were unevenly distributed between plates. Condensate in the plates exacerbated the problem of spreading bacteria.

Dialysis tubing experiment for sediment preference — Two tanks were set up as in group selection experiments with the following changes. Two cups in each tank contained a 5-cm length of dialysis tubing (flat width 43 mm, molecular weight cut off: 12 000–14 000) filled with sieved KC sediment and tied off. The other two cups contained a dialysis tube filled with HP sand. The bag was supported inside the cup with HP sand. If the selection of KC sediment requires only a dispersion of subprotein-sized particles (amino acids, oligosaccharides, for example) worms should be attracted to the diffusion bags containing KC sediment and position themselves in close proximity around it or reject it upon finding that it cannot be inhabited.

Three hundred worms (both *T. tubifex* and *L. hoffmeisteri*) were placed at the epicenter of each tank at the beginning of the experiment and left for 10 d. Worms in each cup were then counted and the numbers for duplicate cups in each tank summed. The *G*-test with Yates' correction factor was used to determine goodness-of-fit with an even distribution of worms.

Manipulation of bacterial abundance — Experimental design was as in group selection experiments except that the contents of the cups were different. Two cups in each tank contained autoclaved KC sediment (KC_A) and the other two contained KC_A which had been inoculated with KC bacteria (KC_{A+B}). Inoculation was accomplished by adding an amount

TABLE 1. Preference of Keating Channel (KC) sediment over Hanlan's Point (HP) sediment by groups composed of *T. tubifex* and *L. hoffmeisteri*. Tests for independence of species and preference and for goodness-of-fit are shown. Worms used in experiments 1, 2, and 3 were collected at Keating Channel. Worms used in experiments 4 and 5 were collected at Hanlan's Point. ***$P < 0.005$; n.s. = $P > 0.05$.

Experiment number	Tank number	Species	Number of worms		Independence G	Goodness-of-fit G[a]
			KC sediment	HP sediment		
1	1	Tt	87	2	n.s.	***
		Lh	41	3		
	2	Tt	32	34	[b]	n.s.
		Lh	7	1		
2	1	Tt	85	42	n.s.	***
		Lh	18	18		
	2	Tt	97	37	n.s.	***
		Lh	31	12		
3	1	Tt	53	12	n.s.	***
		Lh	32	4		
	2	Tt	27	14	n.s.	***
		Lh	21	3		
4	1	Tt	0	1	[b]	***
		Lh	150	13		
	2	Tt	19	2	n.s.	***
		Lh	105	9		
5	1	Tt	5	0	[b]	***
		Lh	131	22		
	2	Tt	9	0	[b]	***
		Lh	113	28		
			$\Sigma = 1063$	$\Sigma = 257$		

[a]Ho: total number of worms (Tt + Lh) choosing KC sediment = total number choosing HP sediment.

[b]Low expected frequencies (i.e. < 5) prevent test of independence.

of the natural KC sediment equal to 5% of the volume of KC_A and holding it aerated at 14°C for 5 d in a covered beaker. This method would introduce other microorganisms besides bacteria.

Two hundred worms (*T. tubifex* and *L. hoffmeisteri*) were placed at the epicenter of each tank to start the experiment. The duration of all experiments was 7 d. Bacterial abundance in sediments was not determined in experiment 1, but was determined at 0, 3, and 7 d in experiment 2 and at 0, 2, and 7 d in experiment 3. Only 0.2 mL of diluted sediment was spread on agar plates to reduce bacterial spreading. Also, agar plates were cracked open and dried for 0.5 h at 35°C before and after inoculation. Just prior to inoculation wet lids were wiped dry with sterile cotton gauze. Plates prepared of autoclaved sediment before it was added to cups showed that there was negligible contamination at this stage. Worm preference was recorded at 7 d for experiment 1, at 3 and 7 d for experiment 2, and at 2 and 7 d for experiment 3.

Two control tanks were set up in experiment 2, one harvested at 3 d and the other at 7 d, in which all four cups contained KC_A. These control tanks were to show how evenly worms dispersed when all cups were identical.

Results

GROUP SELECTION BEHAVIOR

When part of a mixed species group, *T. tubifex* and *L. hoffmeisteri* do not differ in the degree of their preference for KC sediment versus HP sediment (tests of independence, Table 1). This is true whether the worms are collected from Keating Channel (experiments 1, 2, and 3) or Hanlan's Point (experiments 4 and 5). When the data for experiments 1, 2, and 3 (KC worms) are pooled, preference remains independent of species ($G = 2.318$, n.s.). Similarly, when the data for experiments 4 and 5 (HP worms) are pooled, species and preference are independent ($G = 0.632$, n.s.). Therefore, the two species have been combined for tests of goodness-of-fit.

Goodness-of-fit tests (Table 1) show that there is a highly significant preference for one sediment type or the other in all tanks except tank 2, experiment 1. This preference is for KC sediment over HP sediment in every case.

The goodness-of-fit test assumes that individual choice is not influenced by the group. Alternatively, if we assume group influence, it is necessary to treat each tank as if it were a separate trial in an experiment with 10 trials. The calculated probability of obtaining higher numbers of worms in KC sediment in 9 out of 10 trials if there were no preference plus the probability of the less likely event of higher numbers of worms in KC sediment in 10 out of 10 trials is approximately equal to 0.01.

The total number of worms choosing each sediment type is given at the bottom of Table 1 to indicate the overall degree of preference for KC sediment.

SUBSTRATE SELECTION BY INDIVIDUALS

Individual *T. tubifex* show the same preference for KC

TABLE 2. Substrate selection by individual *T. tubifex* with *G*-test for goodness-of-fit. *$P < 0.05$.

Run number	Number of worms	
	KC sediment	HP sediment
1	3	1
2	8	2
3	8	2
4	6	4
5	6	3
6	5	5
7	5	5
Total	41	22*

TABLE 3. Mean percent organic content in Keating Channel and Hanlan's Point sediments.

Collection date	Hanlan's Point		Keating Channel	
	$\bar{x}(n)$	SE	$\bar{x}(n)$	SE
June 7, 1979	9.32(4)	0.75	8.15(4)	0.11
August 8, 1979	10.14(4)	0.77	7.45(4)	0.17
May 26, 1980	5.25(6)	0.07	6.10(6)	0.09
July 3, 1980	7.70(6)	0.01	5.43(6)	0.12

sediment over HP sediment that is characteristic of mixed groups of *T. tubifex* and *L. hoffmeisteri* (Table 2). The probability of obtaining the result shown in Table 2 when there is no preference is less than 0.025. In two of the seven runs, however, there is no preference for either sediment type.

About half of the worms entered a cup and started to burrow within 5 min. Most of the remaining ones made a choice within 20 min, sometimes after changing direction 180° several times, and a small number remained motionless or vacillated back and forth in the tube for a longer period of time before entering a cup. After 2 d all worms were found in one cup or the other. Only 3 worms out of 63 were not in the cup they first entered. Therefore most worms moved directly towards the substrate of their choice (i.e. taxis) rather than settling in it after a random exploration (i.e. kinesis).

SEDIMENT CHARACTERISTICS

Organic content, element analysis, and particle size — Percent organic content of HP sediment was higher than that of KC sediment on three out of four sampling dates (Table 3). Only on May 26, 1980 was the value for KC sediment slightly higher than for HP sediment.

Values for all elements analyzed (Table 4) are higher at Hanlan's Point than at Keating Channel. Only nitrate nitrogen concentrations are virtually the same.

Particle size of both sediments is distributed over the entire range from 500 μm diameter to less than 0.75 μm diameter (Table 5). Keating Channel has a greater percentage of small particles (i.e. silt: 39–62.5 μm diameter and clay: > 3.9 μm diameter) than Hanlan's Point and Hanlan's Point has a greater percentage of sand (> 62.5 μm diameter) than Keating Channel.

TABLE 4. Concentration of selected elements in Keating Channel and Hanlan's Point sediments. Values are in μg g^{-1} of dry sediment.

Element	Keating Channel			Hanlan's Point		
	$\bar{x}(n)$		SE	$\bar{x}(n)$		SE
P (total)	1026	(4)	37	1736	(4)	38
N (nitrate)	7590	(4)	430	7900	(4)	2200
Na	305.8	(4)	6.8	399	(4)	24
Cu	43.5	(4)	4.6	84.0	(2)	3.0
Pb	169	(4)	21	320	(2)	30
Zn	198	(4)	20	375	(2)	35
Mn	318	(4)	30	427	(2)	17
Fe	15400	(4)	1600	25600	(2)	2000
Ni	28	(4)	2.5	46.0	(2)	4.0
Co	14.0	(4)	1.5	23.5	(2)	1.5
Cd	2.63	(4)	0.18	6.65	(2)	0.050

Estimate of bacterial abundance — The mean number of CFU mL^{-1} was 6.57×10^6 for KC sediment ($n = 6$, variance = 27.88×10^6) and 1.77×10^6 for HP sediment ($n = 3$, variance = 0.34×10^6). Variances are too heterogenous to test if this difference is statistically significant. Transformation (ln) of the data reduced heteroscedasticity (KC sediment: $\bar{x} = 1.57 \times 10^6$ CFU mL^{-1}, variance = 0.82; HP sediment: $\bar{x} = 0.53$ CFU mL^{-1}, variance = 0.13) and one-way analysis of variance indicated that the difference between means is not significant ($F = 3.44$, $P > 0.1$ for observed outcome if means are the same). Another assessment of relative bacterial densities was provided by the observation that it was always necessary to dilute KC sediment more than HP sediment in order to obtain countable plates. This observation suggests that the number of bacteria in KC sediment is higher than in HP sediment.

Dialysis tubing experiment for sediment preference — Approximately equal numbers of worms were found in cups containing KC sediment tubes and cups containing HP sediment tubes (Table 6), indicating that there is no preference for either sediment type ($P > 0.05$). This suggests that dialysis tubing interfered with the expression of preference for KC sediment. We thought that worms might be initially attracted to the KC sediment contained in dialysis tubing and then reject it upon finding that it could not be inhabited. This initial attraction was not observed during a daily examination of the tanks. Even at the beginning of the experiment, worms dispersed evenly throughout the tank.

Manipulation of bacterial abundance — A summary of worm preferences and tests of significance for the experiments in which worms were offered a choice of KC_A or KC_{A+B} sediment is given in Table 7. Only the bacteria sampling schedule differed in these experiments. The number of worms found in KC_{A+B} is higher than the number found in KC_A in all tanks except one. The proportion of worms found in KC_{A+B} is significantly different from 0.5 in 6 out of 10 tanks. In no case is there a strong preference for KC_A. KC_A sediment was colonized by large numbers of bacteria from the nonsterile areas of the aquarium during the course of the experiment, but bacterial abundance in KC_{A+B} sediment remained higher throughout.

TABLE 5. Particle size of Hanlan's Point and Keating Channel sediments. $n = 4$ except for the Keating Channel size range of 250–500 μm where $n = 3$.

	Percent of sediment dry weight			
	Hanlan's Point		Keating Channel	
Particle size (diameter, μm)	$\bar{x}$	SE	$\bar{x}$	SE
500–600	0	—	0	—
250–500	3.57	0.39	2.52	0.41
125–250	22.22	0.16	8.78	0.51
63–125	17.80	0.42	6.45	0.18
36–63	18.85	3.14	21.46	2.98
12–36	4.51	0.41	6.66	0.84
6–12	3.18	0.46	5.27	1.20
3–6	5.01	0.88	7.60	1.62
1.5–3	4.53	0.46	6.23	0.57
0.75–1.5	4.07	0.35	6.23	1.14
<0.75	16.27	3.31	28.80	2.56

TABLE 6. Influence of dispersion of subprotein-sized particles on substrate selection by mixed species groups of *T. tubifex* and *L. hoffmeisteri*. The choice is between cups containing Keating Channel sediment enclosed in dialysis tubing and cups containing Hanlan's Point sand enclosed in dialysis tubing.

	Number of worms		
Tank number	KC sediment	HP sand	G
1	52	68	n.s.
2	85	81	n.s.

TABLE 7. Choice of autoclaved Keating Channel sediment (KC_A) versus autoclaved Keating Channel sediment inoculated with bacteria (KC_{A+B}) by mixed species groups of *T. tubifex* and *L. hoffmeisteri*. Shown are total numbers of tubificids harvested in each substrate type and G-tests of goodness-of-fit. $^{**}P < 0.01$; $^{***}P < 0.005$; n.s. = $P > 0.05$.

Experiment number	Tank number	Duration (d)	Substrate type		
			KC_A	KC_{A+B}	G
1	1	7	75	74	n.s.
	2	7	55	67	n.s.
2	1	3	28	61	***
	2	3	18	59	***
	3	7	44	84	***
	4	7	44	82	***
3	1	2	20	22	n.s.
	4	2	24	47	**
	2	7	34	63	***
	3	7	52	54	n.s.

The control tanks unexpectedly provided evidence that worms are not strongly attracted to substrates with low numbers of bacteria. In the control tanks, all four cups contained KC_A sediment; therefore, relatively few bacteria were available to colonize the autoclaved sediment. The sand supporting the cups and the surrounding water would be the main sources of invading bacteria. This situation contrasts with the treatment tanks in which the KC_A cups may be colonized from the KC_{A+B} cups. The proportion of the number of worms found in cups to the total number introduced (200) is much smaller for the control tanks (0.2) than for the treatment tanks (0.5). Worms were distributed more evenly between cups in control tanks than in treatment tanks.

The number of worms choosing sediment with varying bacterial content is shown in Fig. 2. The product-moment correlation coefficient for worm preference and bacterial abundance is 0.708, equivalent to $P < 0.01$. We judge that the non-normal distribution of bacterial abundance data (which necessitated a log scale in Fig. 2) can be safely ignored for the purposes of this test because the sample size is small ($n = 13$). The Kendall rank correlation coefficient for worm preference and bacterial abundance is also highly significant ($r = 0.615$; $P = 0.0034$, two tails).

Discussion

Mixed species groups of tubificids collected from either Keating Channel or Hanlan's Point prefer Keating Channel sediment over Hanlan's Point sediment under laboratory conditions. This result contrasts with the examples of habitat selection examined by Meadows and Campbell (1972) in which populations of a species which live in contrasting habitats show preferences in accordance with those contrasts. For example, isopods of the species *Asellus communis* collected from streams are consistently more rheopositive (move towards gravity) than the same species collected from ponds (Allee 1912).

Individual *T. tubifex* also prefer KC sediment. As most worms selected a substrate by moving directly towards it (i.e. taxis), they must be able to detect the presence and direction of a sediment component dispersing through the water. The considerable behavioral heterogeneity of individuals may be accounted for by the existence of differing behavioral types in the population. Individual variation in habitat selection behavior has been found in other invertebrates. For example, emerging larvae of the western tent caterpillar, *Malacosoma pluviale*, are of two behavioral types (Wellington 1957). Type I larvae are active, move in a straight line, and are capable of directed movement towards

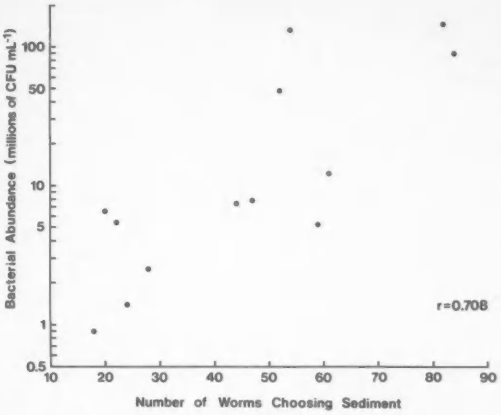

FIG. 2. The number of tubificids (both *T. tubifex* and *L. hoffmeisteri*) choosing sediment of varying bacterial abundance. The correlation is of untransformed variables. CFU = colony-forming units.

a light source. Type II larvae are sluggish, turn aimlessly, and are incapable of directed movement towards a light source unless they follow the trail left by Type I larvae. Some of the advantages and disadvantages associated with the presence of active and inactive behavioral types in the western tent caterpillar would also apply to tubificids. Active individuals, capable of taxis, would be effective at colonizing new habitats, locating new food sources and responding to changing environmental conditions. They might also be more susceptible to mortality by predation and accident than less active worms. Sluggish individuals, incapable of taxis, are perhaps better suited to living under the conditions of extremely high population density which develop in nutrient-rich areas.

A clear distinction must be made between stating that tubificids prefer sediment which is organically polluted (i.e. receives sewage effluent) and stating that tubificids prefer sediment of high organic content. Though the former statement is borne out by this study, the latter is not. HP sediment has a higher organic content over most of the year than does KC sediment. Brinkhurst and Jamieson (1971) have already pointed out that where careful analyses have been made, few clear correlations between the variations of total organic matter and the distribution and abundance of worms have been demonstrated. The quality of organic matter in the sediment is therefore more important in determining tubificid preference than the quantity of organic matter.

The high concentration of phosphorus in HP sediment compared to KC sediment is surprising in light of the large amount of nutrient-rich material deposited at the mouth of Keating Channel where the Don River meets the sluggish harbor waters. The ambient concentration of phosphorus or any other element in sediment is, however, not necessarily related to the rate at which it is being added by sedimentation (Brinkhurst 1972). It is necessary to take into account addition by biological excretion as well as decomposition and removal by sedimentation (rendering some sediment inaccessible), erosion, commercial dredging and biological production. If tubificids select sediment on the basis of ambient phosphorus concentration, it is difficult to understand why they prefer the low phosphorus level of KC sediment to the higher level of HP sediment.

It is unlikely that the difference in iron concentration between HP and KC sediment would result in an avoidance response to HP sediment. Johnson and Matheson (1968) found that *L. hoffmeisteri* and *T. tubifex* were not inhibited in the profundal sediments of the main basin of Hamilton Bay, Lake Ontario, which contained 16–20% Fe_2O_3, a much higher concentration of iron than at Hanlan's Point. The concentrations of other metals are also probably too low to provoke an avoidance response. Copper and zinc provoke such a response at concentrations of 570 and 1140 $\mu g\ g^{-1}$ dry sediment respectively, in KC sediment (McMurtry 1982), however the threshold level is not known.

The subtle differences in particle size between KC and HP sediment are unlikely to account for the preference for KC sediment. Both substrates are predominantly silt (32% for HP and 47% for KC) and both are composed of particles over the same size range. In related work (unpublished data of K. E. Chua and D. J. Rapport) sieved HP sand was added to KC sediment in order to modify particle size. One substrate offered to tubificids in a substrate selection experiment was a mixture of 80% sand from 500–600 μm in diameter and 20% sieved KC sediment. The other substrate offered was 80% sand 212 μm in diameter and 20% sieved KC sediment. Out of eight trials, two came out significantly ($P < 0.05$) in favor of the fine substrate, one came out significantly in favor of the coarse substrate and the others were not significant. If differences in particle size on this scale have no consistent effect on substrate choice, it is unlikely that the more subtle differences between KC and HP sediment are responsible for the repeatedly observed preference for KC sediment.

The direct comparison of heterotrophic aerobic bacterial abundance in HP sediment and KC sediment was inconclusive. Uneven dispersion of sediment in the diluent probably contributed to variability in the data. Improved precision might be obtained by using dispersant such as Triton X 100. In addition, the plate count technique is innately imprecise due to the variable distribution of bacteria on sediment particles (Meadows and Anderson 1968) and in suspension. Only those bacteria contacting the agar surface produce a colony.

Dialysis tubing blocks the movement of whatever substances are responsible for the attractiveness of KC sediment. Subprotein-sized particles are able to pass through dialysis tubing; therefore particles larger than this must account for the preference for KC sediment. This observation together with previously published evidence that bacteria are the major food source of tubificids strongly suggests that bacteria are an important influence on sediment attractiveness.

When bacterial abundance was varied in KC sediment, a strong correlation between abundance of heterotrophic aerobic bacteria and tubificid preference was observed. We conclude that of the sediment characteristics examined the microbial composition of Toronto Harbour sediment is the most important determinant of substrate preference by tubificids. Sediment preference may also be related to the particular species of bacteria present, as Gray and Johnson (1979) have

clearly shown for the marine gastrotrich, *Turbanella hyalina*. The work of Brinkhurst and Chua (1969), Wavre and Brinkhurst (1971), Brinkhurst et al. (1972) and Coler et al. (1967) suggests that this may be the case in tubificids. The role of potential food sources such as anaerobic bacteria, protozoans, and large organic molecules in substrate selection is largely unknown.

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Effect of *P*-Cresol on Leaf Decomposition and Invertebrate Colonization in Experimental Outdoor Streams

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STOUT, R. J., AND W. E. COOPER. 1983. Effect of *p*-cresol on leaf decomposition and invertebrate colonization in experimental outdoor streams. Can. J. Fish. Aquat. Sci. 40: 1647–1657.

In 1980, outdoor experimental stream channels at Monticello, Minnesota were continuously dosed for 24 and later 48 h with 8 mg/L *p*-cresol, a toxic phenolic by-product of coal gasification. The dosage, based on laboratory studies by the Environmental Protection Agency, was expected to stress but not to kill fish and invertebrates in the channels. Two unexpected results occurred: (1) severe depressions in dissolved oxygen (less than 1 mg/L), and (2) mortality to some fish and invertebrate species in the experimental versus reference channels. Because the direct effects on the aquatic ecosystem were inseparable from the indirect effect of reduced dissolved oxygen, two types of dosing regimes were designed in 1981 to partially uncouple the direct from the indirect effects. First, a continuous dose at 8 mg/L for 96 h was administered, then a second intermittent dose at 8 mg/L with temporary cessations when reductions in dissolved oxygen occurred. Leafpacks were placed in experimental and reference channels to monitor community level responses to the toxicant under severe long-term and under moderate short-term dissolved oxygen depletions. Biotic responses to the intermittent dose schedule were less severe than biotic responses to the continuous dose. The intermittently dosed experimental channel and its reference channel were more similar to each other than was the continuously dosed channel as compared with its reference channel with respect to: (1) invertebrate colonization patterns, (2) invertebrate biomass changes over time and (3) leaf biomass changes over time. During the continuous dose, some invertebrate species that were rare colonists on leafpacks became highly abundant (leeches and isopods); other normal colonists became extremely abundant (snails and flatworms) or diminished (freshwater scuds). These changes in colonization patterns significantly altered biomass of invertebrates on leafpacks over time. Leaf biomass losses were similar over time except in the continuously dosed channel where swamp poplar leaf losses (*Populus deltoides* Marsh) were significantly smaller during and shortly after the dose.

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En 1980, des chenaux expérimentaux installés à l'extérieur à Monticello, au Wisconsin, ont été traités de façon continue pendant 24 h, et plus tard, pendant 48 h avec une solution de 8 mg/L de *p*-cresol, un sous-produit phénolique toxique de la gazéification du charbon. Sur la base d'études en laboratoire menées par l'Environmental Protection Agency, le traitement devait produire un stress mais non des mortalités chez les poissons et les invertébrés dans les chenaux. Au lieu de cela, il se produisit deux phénomènes inattendus : (1) sérieuses diminutions d'oxygène dissous (moins de 1 mg/L) et (2) mortalités de certaines espèces de poissons et d'invertébrés dans les chenaux expérimentaux par rapport aux chenaux témoins. Devant l'impossibilité de séparer les effets directs des effets indirects d'une diminution d'oxygène dissous sur l'écosystème aquatique, on a conçu en 1981 deux types de traitements visant à séparer partiellement ces deux groupes d'effets. En premier lieu, on a administré un traitement continu avec 8 mg/L pendant 96 h, suivi d'un second traitement intermittent avec la même concentration, mais avec arrêts temporaires quand diminuait l'oxygène dissous. Des paquets de feuilles furent placés dans les chenaux expérimentaux et dans les chenaux témoins en vue de suivre de façon continue les réactions, au niveau de la communauté, au toxique dans des conditions d'épuisement d'oxygène dissous, sévères et à long terme, d'une part, et modérées et à court terme, d'autre part. Les réactions biologiques au traitement intermittent ont été moins violentes qu'avec le traitement continu. La ressemblance entre le chenal expérimental traité de façon intermittente et son chenal de référence était plus grande que dans

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le cas du chenal traité de façon continue et de son chenal de référence, sous les aspects suivants : (1) modalités de colonisation par les invertébrés, (2) changements temporels de la biomasse d'invertébrés et (3) changements temporels de la biomasse de feuilles. Pendant le traitement continu, certaines espèces d'invertébrés qui étaient de rares colonisateurs de paquets de feuilles devinrent très abondantes (sangsues et isopodes); d'autres colonisateurs normaux devinrent extrêmement abondants (limaçons et vers plats) ou diminuèrent (pucerons d'eau douce). Ces modifications des schémas de colonisation eurent pour effet d'altérer notablement avec le temps la biomasse d'invertébrés sur les paquets de feuilles. Les pertes de biomasse de feuilles ont été identiques dans le temps, sauf dans le chenal soumis au traitement continu et dans lequel les pertes de feuilles de peuplier deltoïde (*Populus deltoides* Marsh) ont été nettement plus faibles pendant et peu après le traitement.

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P-CRESOL is one of a series of phenol-derived by-products from coal gasification processing for energy and from phenol producing plants. Accidental spills of phenolic compounds, including *p*-cresol, have occurred in Europe (Alabaster et al. 1973) with damaging effects on streams and rivers. With the recent development of large-scale coal gasification methods which allowed construction of new plants in the United States (Spencer et al. 1982), risks of accidental spills of phenolic compounds in the United States will increase. This paper describes one in a series of studies on fate and effects of this energy-related toxicant in a stream ecosystem conducted over a 3-yr period (Cooper and Stout 1982; Coleman et al. 1982).

Leaf decomposition and invertebrate colonization patterns onto leaves in stressed streams have been studied extensively (Benfield et al. 1977; Cummins et al. 1973; Iverson 1973; Kaushik and Hynes 1971; Petersen and Cummins 1974; Reice 1974; Short et al. 1980). Both decomposition and colonization processes concern community level responses to changing environments. These processes have been most often studied in unstressed systems; they are also appropriate community level processes for study in toxicologically stressed stream ecosystems. Problems in environmental toxicology necessitate more emphasis at the community level rather than at the single species toxicity test level (Cairns 1981). This study was directed toward community level responses to toxicant stress. We examined: (1) leaf litter processing, (2) invertebrate colonization patterns on leaf litter, and (3) the often used structural descriptors of community change: species richness, species evenness, and species diversity (see Wilhm and Dorris 1966; Sanders 1968; Tramer 1969; Allan 1975; Cornell et al. 1976 for similar studies).

The first type of community level response, leaf litter processing, includes chemical and physical leaching, conditioning by microbial activities, and feeding by macroinvertebrates. Anthropogenic environmental alterations can affect both the chemical and biological phenomena associated with litter processing. For example, Short and Ward (1980) showed that a winter-warm thermal regime in a regulated stream caused alder leaves to decompose at a faster rate than in an unregulated stream, even though the invertebrate shredder guild was more abundant in the latter stream. They suggest that the microbial fraction was likely more active in the warmer waters of the regulated stream.

The second community level response, colonization by invertebrates onto leaf litter, indicates community resiliency to perturbations. By looking at colonization patterns one can observe sublethal, behavioral responses due to environmental changes as well as direct lethal effects. Gersich and Brusven (1981) showed that rocks below the Dworshak Dam in Idaho required approximately 66 d to reach invertebrate carrying capacity, while only 47 d were required for rocks placed in an undammed reach of the river.

The third community level response, structural community indices, have often been used as primary indices for documentation of community change. We compare species diversity, species richness, and species evenness indices with biomass and individual species changes in the analyses of the invertebrate leafpack community data.

Materials and Methods

Site Description and Dosing Regime

The outdoor stream channels at Monticello, Minnesota, contained recirculating water which could be filled with either Mississippi River water or well water or a combination of both. The streams, each 1000 m long, average 3.22 m wide and 0.39 m deep along the 30 m riffle sections and 3.86 m wide and 0.86 m deep along the 30 m pool sections. The experimentally controlled mean velocity during the study was 6.4 cm/s and the mean water temperature was 23.2°C with an average diurnal variation of 4.9°C. Continuous monitoring, including *p*-cresol concentration, dissolved oxygen, pH, temperature, velocity, depth and solar radiation, was done along the stream channels throughout the study.

P-cresol (99^{+}% pure, Aldrich Chemical Co.) was introduced into one of the channels continuously to maintain 8 mg/L for 96 h from 29 June to 3 July, 1981. An adjacent channel was used as the reference channel. In the intermittent dose, *p*-cresol was injected three times: on 19 July for 6.75 h; on 21 July for 7.5 h and on 23 July for 6.5 h for a total exposure equal to a continuous 48-h dose at 8 mg/L.

Background for Leafpack Experiments

In 1980 we had observed mortality of certain species of aquatic invertebrates and fish when we added *p*-cresol at 8 mg/L for 48 h in those channels (Cooper and Stout 1982). Dissolved oxygen (D.O.) concentrations dropped to less than 1 mg/L in the channel toward the end of the dose just

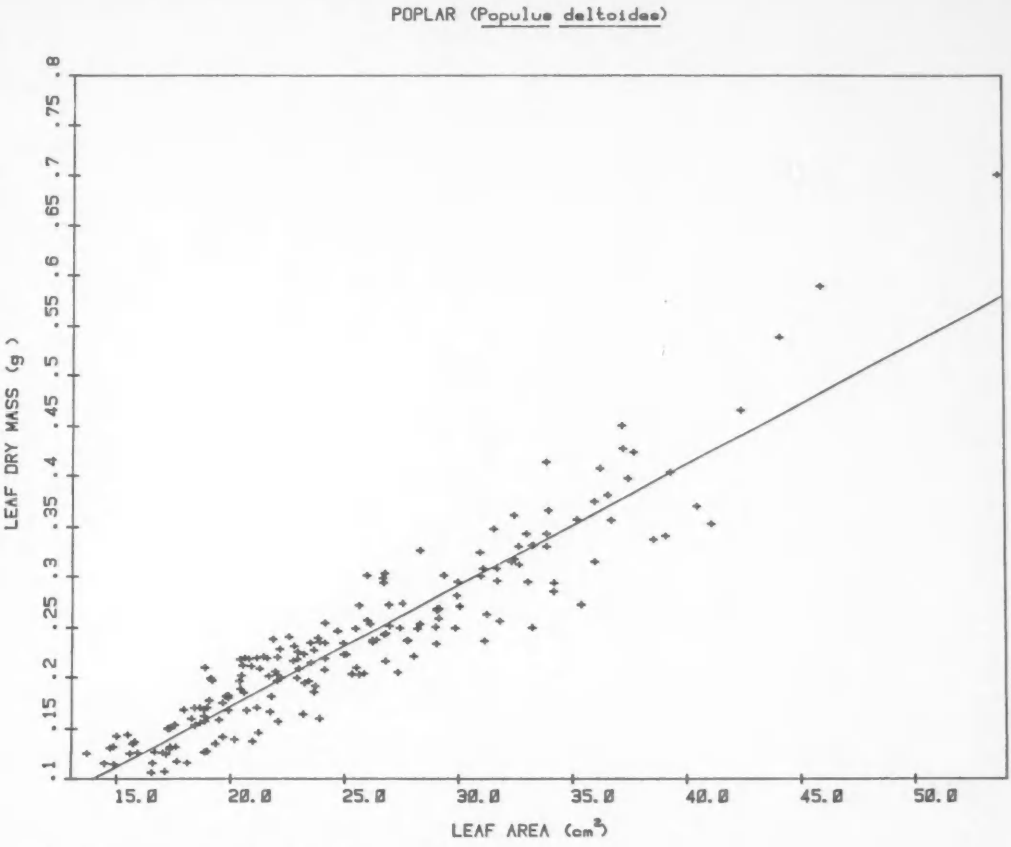

FIG. 1. Relationship between leaf area (cm^2) and dry mass (g) of poplar leaves.

prior to the pronounced biotic effects. This result was unexpected as laboratory tests (in which oxygen was bubbled into the tanks) indicated that higher concentrations would be necessary.

The channels were highly autotrophic ($P/R > 1$), the principal primary producer being a filamentous green alga, *Spirogyra* sp. Because the alga showed signs of a stress toward the end of the 48-h dose (i.e. a browning of the filaments), we performed photosynthetic and respiration rate experiments on the alga with and without *p*-cresol. The photosynthetic rate decreased and the respiration rate increased after 2 h incubation with *p*-cresol (Stout and Kilham 1983). Additonal experiments at the site showed that the alga turned brown after 1 h incubation in *p*-cresol at concentrations of 14, 34, and 71 mg/L, but remained green at *p*-cresol concentrations of 0.9 and 1.6 mg/L (D. Mount and T. Norberg, EPA, Duluth Labs, MN). We therefore ran two experimental dosing schedules in 1981: (1) a continuous dose over a 96- rather than a 48-h period, and (2) an intermittent dose where we monitored dissolved oxygen carefully, stopping injection of *p*-cresol prior to extreme drops in D.O. We wanted to uncouple effects of the toxicant from low D.O. so we could compare the two types of effects. The leafpacks placed in the channels in 1981 were used to study community changes in leaf litter processing and in invertebrate colonization patterns under, (1) oxygen and toxicant stress conditions (continuous 96-h dose), and (2) under similar toxicant stress with reduced oxygen stress (intermittent dose).

PROCEDURE

Two experiments were performed prior to the major study to ascertain decomposition rates for oven-dried versus undried fresh poplar leaves and to determine the relationship between initial leaf area and dry weight of poplar leaves so that, if necessary, estimates of initial dry weights could be made without drying leaves. In the first experiment, one set of leaves was measured for area to the nearest mm^2, put into

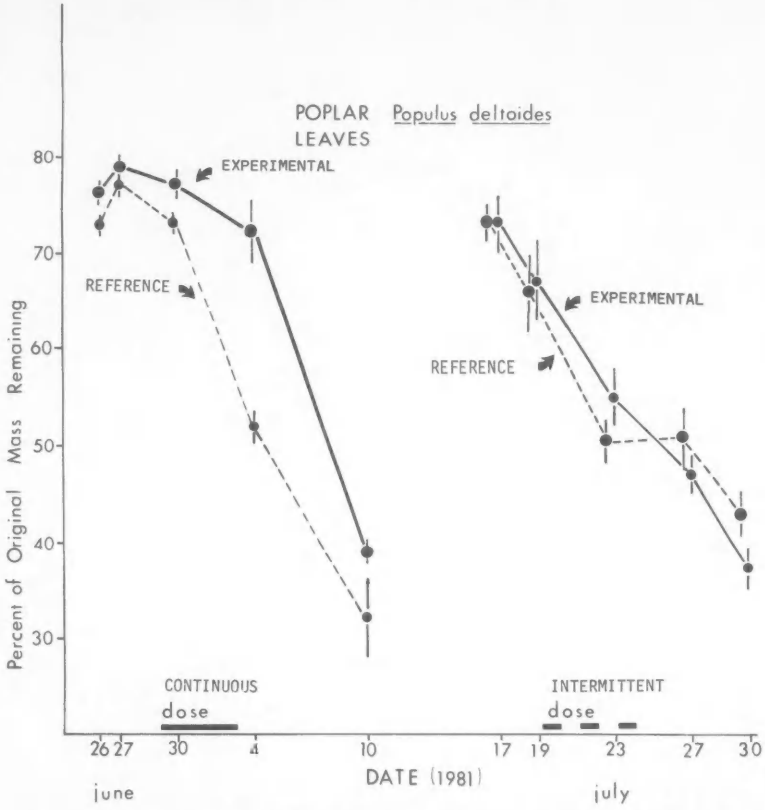

FIG. 2. Percent dry mass loss of poplar leafpacks for continuous and intermittent dose experiments. Solid lines = experimental channels, broken lines = reference channels. Vertical bars = standard error about the mean.

30 leafpacks of 10 leaves each, and dried at 100°C for 24 h. Another set of fresh leaves was measured for area the same day the dried set was weighed. Both sets were then conditioned for 24 h and placed in the control stream channel. Three replicates of each treatment were gathered five times over a 19-d period, washed, measured for leaf area, dried, and weighed to determine the final dry weights. In the second experiment, 200 poplar leaves were numerically coded, measured for leaf area, dried, and weighed. A linear regression analysis was performed on the data to determine the relationship between initial area and initial dry weight. Results from these experiments led us to use dry mass changes rather than leaf area changes for the major set of experiments because most of the activity on the leaves was by leaf surface feeders and the leaf area meter could not detect surface mining. Use of leaf area measurements was limited to the calculation of the initial dry mass estimates for fresh leaves.

Green leaves from the swamp poplar (*Populus deltoides* Marsh) and burr oak (*Quercus macrocarpa* Michx.) were collected at the site from a single tree for each species to minimize individual leaf variation. The surface area of each leaf was measured with a Licor Model LI-3000 leaf area meter. Leafpacks containing 10 leaves each were made, bagged in 60-m mesh Tygon® netting and conditioned for 48 h in a 2 m diameter tank containing filtered circulating channel water. After 48 h, leaves were removed from the bags and lashed to bricks with monofilament line. The bricks were placed in a riffle section of each channel, with leaves facing the stream current. The bricks were kept free of debris and filamentous algae as much as possible. For the continuous dose, three replicates of poplar and three replicates of oak leafpacks were taken from the channels five times over a 16-d period. For the intermittent dose, samples were collected five times over a 15-d period.

On days of collection, bricks were lifted from the streams, and held above a bucket containing channel water to catch any active invertebrates leaving the pack. The monofilament line was cut and leaves were placed in plastic bags. After the

TABLE 1. Processing coefficients (k) for poplar (*P. deltoides*) leaves. (Mean temperature: 23.2°C).

Dose type	k	r^2
Continuous dose		
Reference channel	0.0615	0.924
Experimental channel	0.0460	0.772
Intermittent dose		
Reference channel	0.0375	0.908
Experimental channel	0.0502	0.984

leaves were removed, the face of the brick was washed in the bucket. Both the leaves and tagged sample buckets were immediately carried to an outdoor washing table where leaves and collected water were carefully washed above a 60-μm mesh sieve. Invertebrates were preserved in 10% formalin and leaves were returned to the laboratory for surface area measurements. They were then oven-dried at 100°C for 24 h and weighed to the nearest milligram.

Results

Leaf Decomposition

Preliminary experiments — Swamp poplar leaves decomposed rapidly. After 8 d, oven-dried leaves lost over 50% of their dry mass, while undried leaves lost only 15% of their dry mass. We therefore chose fresh leaves for experiments since dried leaves decomposed too fast for our purposes.

Linear regression analysis (Fig. 1) of leaf area versus dry mass ($r^2 = 0.88$) indicates initial dry mass values can be estimated from leaf area.

Experiments with and without p-*cresol* — Percent dry weight loss over time for poplar leaves was lower in the experimental channel than in the reference channel during the 96-h continuous dose experiment (Fig. 2). The processing coefficients (k) following a $\log_e$ transformation of the data were computed after Petersen and Cummins (1974) and appear in Table 1. (Losses due to leaching were included in the estimates for k for these fresh leaves.) The k values for the poplar were high, indicating very fast processing rates (see Short and Ward 1980 for comparison with other published k values). Leaves placed in the experimental stream during the 96-h continuous dosing had the lowest r^2 value for the linear regression, owing to the greatest point deviation that occurred just after cessation of the dose (4 July). If the curve for leaf decomposition in the experimental channel is shifted back 4 d (the duration of the dose), the results from the experimental channel approximate those from the reference stream, indicating fast recovery for poplar leaves after 4 July.

Results for poplar leaves were similar in both the experimental and reference channel for the intermittent dose experiment. Although the reference channel had been previously dosed with *p*-cresol, no *p*-cresol remained 24 h after dose cessation, dissolved oxygen returned to normal levels within 4 d after the dose (Fig. 3) and invertebrate densities in substrate samplers (23 × 8 cm) had returned to normal levels after 3 d except for the water scud, *Hyalella azteca* (see Table 2). (Mississippi water, containing potential recolonists, had been pumped through both channels for 10 d prior to the intermittent dose.)

Oak leaves did not decompose significantly (as determined from dry mass and leaf area values) during each of the two experiments and were not considered in the analysis.

Colonization of Invertebrates on Leafpacks

The general colonization pattern for invertebrates onto leafpacks was similar for both poplar and oak leaves, except that on average, there were more individuals and species on oak than on poplar leaves over time (Tables 3 and 4). Oak leaves are more stable over time, chemically different, and larger than poplar leaves (initial mean leaf area for poplar: 26.65 cm^2; SE = 0.42, n = 282; initial mean leaf area for oak: 41.94 cm^2; SE = 0.79, n = 280). The relative change in numbers of individuals and species for oak and poplar are related to temporal factors and to the 96-h continuous dosing experiment. Under non-dosing conditions, the numbers of individuals and species increased for the first 8–10 d, and then decreased as the poplar leaves approached 50% of original dry mass. On oak, numbers continued to increase, likely owing to the temporally stable leaf mass.

Poplar leaves were over 55% processed by the end of each of the dosing experiments. The number of invertebrate species and individuals on those leaves also declined from midpoint (middle of dose) levels in the channels; however, the drop in numbers was greater in the experimental channels (Table 3). By looking only at structural community indices (species richness, evenness, and species diversity), one would theorize that during the dose, more species were added equitably onto the leaves. Yet, more meaningful data appear if one looks at changes for individual species, both in terms of numbers and biomass. During the dose, numbers of individuals of the scud, *Hyalella azteca*, dropped from pre-dose numbers and never recovered. Numbers of flatworms, *Planaria* sp., in reference channels increased on leaves over time, but during both doses, numbers increased 20 to over 30-fold and then dropped after the doses. There was an 8-fold increase in numbers of snails, *Physa*, during the continuous dose, but after, the numbers returned to pre-dose levels. Leeches, Hirudinea and isopods, *Asellus* sp., although uncommon on leaves, were highly abundant only during the continuous dose. Snails and isopods are high in mass and therefore have a larger impact on total biomass values than on the evenness index (Compare Table 3 and 4 with Fig. 5). Although the structural community indices reflected the effects of the dosings, individual species and biomass changes gave more information regarding the dynamics of community shifts.

Oak leaves hardly decomposed during either experiment. Numbers of species and numbers of individuals on control leafpacks continued to increase over time (Table 4). Only experimental leafpacks, after the continuous dose experiment, had lower numbers of species and individuals. For four species, some of the more revealing changes occurred during, as compared with after, the continuous dose: as for the poplar leafpacks, numbers of *H. azteca* were lower during the dose in the experimental channel than were numbers at the pre-dose; snails increased 20-fold as compared to a less than

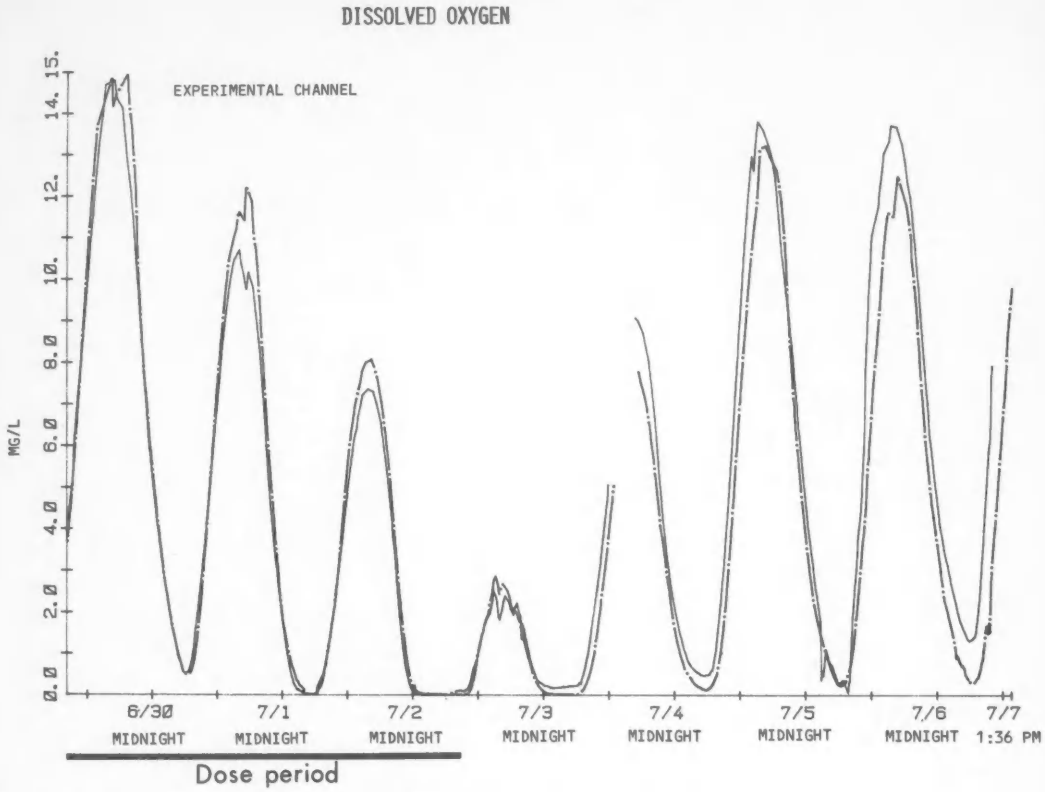

FIG. 3. D.O. (mg/L) at two locations in experimental channel during 96-h continuous dose.

TABLE 2. Average numbers of invertebrates in substrate samples from riffles at sites where leafpacks were placed.

	Channel for continuous dose			Channel for intermittent dose		
Date	*Hyalella azteca*	Other inverts.	Total numbers	*Hyalella azteca*	Other inverts.	Total numbers
6/20	1522	167	1689	1411	410	1190
6/28	989	192	1181	1026	338	1346
7/1	833	171	1004	1152	246	1398
7/3	537	305	842	1020	220	1240
7/6	512	251	763	1857	315	2172
7/16	447	310	748	2059	331	2390
7/21	350	242	592	3759	282	4042
7/26	626	226	842	1493	466	1959
7/30	682	268	950	859	328	1687

one-fold increase for the reference channel, and isopods and leeches became a significant component of the invertebrate leafpack community only in the experimental leafpacks (Table 4). No analogous results were found for the intermittent dose experiment.

The most common animal colonizing the leaf packs was *H. azteca*. In the laboratory, it showed a 44% mortality rate after 96 h exposure to 5 mg/L *p*-cresol in aerated water (5.5 mg/L or more D.O.). The 96-h LC_{50} was less than 2 mg/L *p*-cresol (Cooper and Stout 1982). These animals

TABLE 3. Mean numbers of invertebrates per poplar leafpack (± standard error) for a 96-h continuous dose and an intermittent dose of *p*-cresol at 8 mg/L.

	Continuous dose						Intermittent dose					
	Reference channel dose			Experimental channel dose			Reference channel dose			Experimental channel dose		
Abundances of selected invertebrates	Before (6/27)	Endpoint (7/04)	After (7/10)	Before (6/27)	Endpoint (7/04)	After (7/10)	Before (7/17)	Endpoint (7/23)	After (7/30)	Before (7/17)	Endpoint (7/23)	After (7/30)
Hyalella azteca	161.5 (70.7)	194.0 (64.3)	105.7 (27.8)	48.5 (1.5)	38.3 (18.8)	9.7 (1.9)	3.7 (0.3)	30.7 (10.8)	18.0 (4.6)	64.7 (9.0)	102.0 (2.1)	56.9 (18.2)
Planaria sp.	2.0 (1.0)	14.0 (2.1)	25.3 (3.9)	2.5 (0.5)	46.0 (28.6)	3.0 (0.6)	1.7 (0.7)	15.3 (4.3)	10.3 (2.3)	13.0 (7.2)	99.7 (29.8)	23.0 (12.1)
Physa sp.	4.0 (2.0)	8.7 (2.7)	10.7 (0.7)	9.0 (3.0)	71.0 (29.5)	7.0 (1.2)	3.0 (1.5)	15.0 (3.5)	4.3 (2.2)	7.0 (1.0)	23.0 (3.8)	12.0 (6.0)
Asellus sp.	0	0	0	0	19.0 (7.7)	0	0	1.7	1.7	0	0.7	0
Hirudinea	0	0	0	0.5	14.0 (1.5)	0	0	0	0	0	1.3	0
Community structural indices												
Total number of individuals	173.0 (98.2)	230.0 (68.9)	155.7 (34.6)	62.5 (4.5)	190.3 (71.2)	21.0 (3.5)	13.3 (7.7)	71.0 (17.1)	40.3 (0.3)	88.3 (3.5)	238.7 (29.8)	115.0 (21.4)
Species richness (S)	5.5 (1.5)	7.0 (0.0)	6.3 (0.9)	5.5 (0.5)	6.3 (0.9)	3.7 (0.7)	5.3 (1.4)	7.7 (0.3)	7.7 (0.3)	4.7 (0.3)	8.3 (0.2)	7.3 (0.3)
Evenness (J′)	0.18 (0.02)	0.36 (0.04)	0.60 (0.06)	0.45 (0.04)	0.78 (0.06)	0.90 (0.04)	0.87 (0.01)	0.74 (0.05)	0.71 (0.06)	0.51 (0.08)	0.56 (0.01)	0.64 (0.04)
Species diversity (H′)	0.43 (0.12)	1.02 (0.13)	1.55 (0.07)	1.10 (0.04)	2.14 (0.09)	1.63 (0.14)	2.00 (0.34)	2.17 (0.11)	2.10 (0.20)	1.13 (0.22)	1.70 (0.05)	1.84 (0.17)

TABLE 4. Mean numbers of invertebrates per oak leafpack (± standard error) for a continuous dose and an intermittent dose of *p*-cresol at 8 mg/L.

	Continuous dose						Intermittent dose					
	Reference channel dose			Experimental channel dose			Reference channel dose			Experimental channel dose		
Abundances of selected invertebrates	Before (6/27)	Endpoint (7/04)	After (7/10)	Before (6/27)	Endpoint (7/04)	After (7/10)	Before (7/18)	Endpoint (7/24)	After (7/30)	Before (7/18)	Endpoint (7/24)	After (7/30)
Hyalella azteca	164.5 (7.5)	303.0 (14.2)	375.7 (77.3)	81.0 (17.0)	27.7 (11.3)	55.7 (5.8)	8.7 (2.7)	40.0 (10.2)	36.0 (4.4)	63.7 (6.7)	124.3 (39.4)	158.0 (20.1)
Planaria sp.	6.0 (1.4)	20.7 (12.2)	29.0 (14.0)	3.0 (3.0)	28.0 (12.6)	11.3 (3.5)	0 (0)	14.0 (4.4)	32.0 (11.6)	3.0 (1.0)	109.3 (29.3)	57.7 (11.6)
Physa sp.	4.5 (1.5)	6.3 (0.9)	13.3 (3.5)	6.0 (1.0)	128.0 (29.7)	6.3 (3.7)	6.3 (1.9)	8.7 (2.6)	12.7 (5.2)	7.3 (0.9)	17.7 (7.4)	13.7 (5.2)
Asellus sp.	0	0.7	0	0.5	48.7 (24.3)	1.7	0.7	1.3	1.7	0	5.0 (2.3)	0
Hirudinea	0.5	0	0.3	2.0	46.3 (19.5)	0.7	1.0	0.7	0.7	0	0	0
Community structural indices												
Total number of individuals	181.0 (8.0)	348.7 (12.4)	446.3 (96.7)	97.0 (16.0)	287.0 (46.6)	70.3 (13.4)	24.3 (4.4)	76.7 (16.3)	99.7 (23.2)	77.3 (6.2)	262.7 (48.0)	247.7 (21.1)
Species richness (S)	5.5 (1.5)	6.3 (0.7)	9.7 (1.8)	6.5 (1.5)	10.0 (0.6)	5.7 (0.7)	7.3 (0.7)	8.0 (1.2)	9.3 (1.2)	5.7 (0.9)	6.0 (1.2)	8.7 (1.2)
Evenness (J′)	0.26 (0.03)	0.29 (0.07)	0.30 (0.02)	0.48 (0.04)	0.63 (0.01)	0.56 (0.02)	0.84 (0.06)	0.67 (0.01)	0.71 (0.01)	0.40 (0.02)	0.61 (0.06)	0.50 (0.04)
Species diversity (H′)	0.61 (0.04)	0.76 (0.13)	0.98 (0.12)	1.00 (0.10)	2.08 (0.02)	1.41 (0.12)	2.39 (0.12)	1.99 (0.11)	2.28 (0.04)	0.99 (0.11)	1.84 (0.19)	1.55 (0.14)

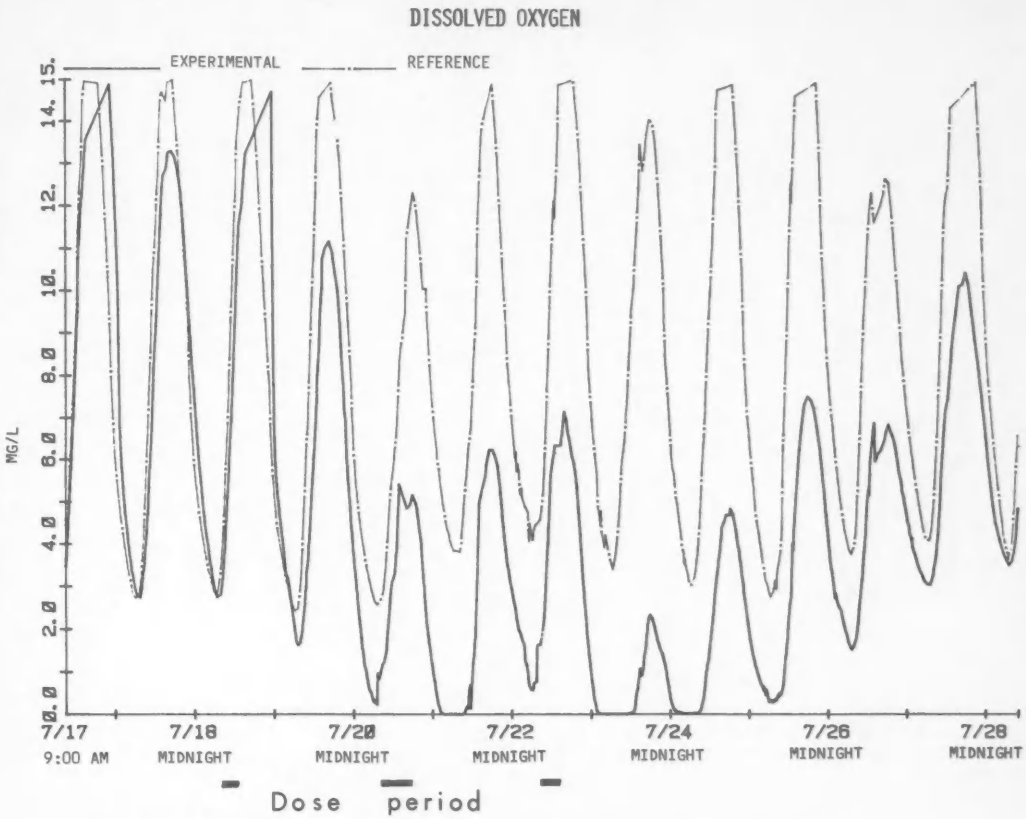

FIG. 4. D.O. (mg/L) in experimental channel (solid lines) and reference channel (broken lines) during the pulsed dose.

also showed an adverse effect under field conditions, both reflected by their lowered numbers on leafpacks after 96 h of continuous exposure to *p*-cresol and by our observing dead animals on floating filamentous algal mats.

In the lab, D. Mount (EPA Duluth Labs, MN) observed a 12% mortality rate for these animals after 48 h of exposure to 5 mg/L *p*-cresol. Given the fact that the experimental channel had time to recover some dissolved oxygen between pulses, it is reasonable to presume that the intermittent dose should have only a moderate mortality effect on *H. azteca*. Its numbers were higher in experimental leafpacks at the midpoint of the intermittent dose as compared with pre-dose levels. It is possible that the scuds had sufficient time between dosings to depurate *p*-cresol. Fish tested for bioaccumulation of *p*-cresol in the experimental channel during the continuous dose depurated *p*-cresol within 24 h (Cooper and Stout 1982). No dead scuds were observed on algal mats during the intermittent dose and there were no prolonged periods of anaerobic conditions.

During non-dosing periods, the isopod, *Asellus* sp., was usually found among root mats of emergent grasses and sedges. Forty-eight h into the continuous dose when the D.O. dropped to very low levels for over 8 h each night (Fig. 3), animals left their usual habitat and entered the water column and leafpacks. They were not usual colonizers on leaves. During the intermittent dose, however, very few isopods entered leafpacks. Dissolved oxygen fell to very low levels for a maximum of 5 h (Fig. 4). Mount and Norberg (EPA Duluth Labs, MN) showed that the 96 h LC_{50} for these animals was associated with the lowered dissolved oxygen tension rather than with *p*-cresol concentration. Because leeches did not enter leafpacks during the intermittent dose, their entry onto leafpacks during the continuous dose probably is also more related to low dissolved oxygen rather than to the toxicant itself.

Physa sp., a pulmonate snail, accounted for the marked biomass increase on leaves in the experimental channel during the continuous dose. *Physa* were normal colonists on leaves, but their numbers increased 8-fold on poplar leafpacks and 20-fold on oak leafpacks in the experimental channel at the

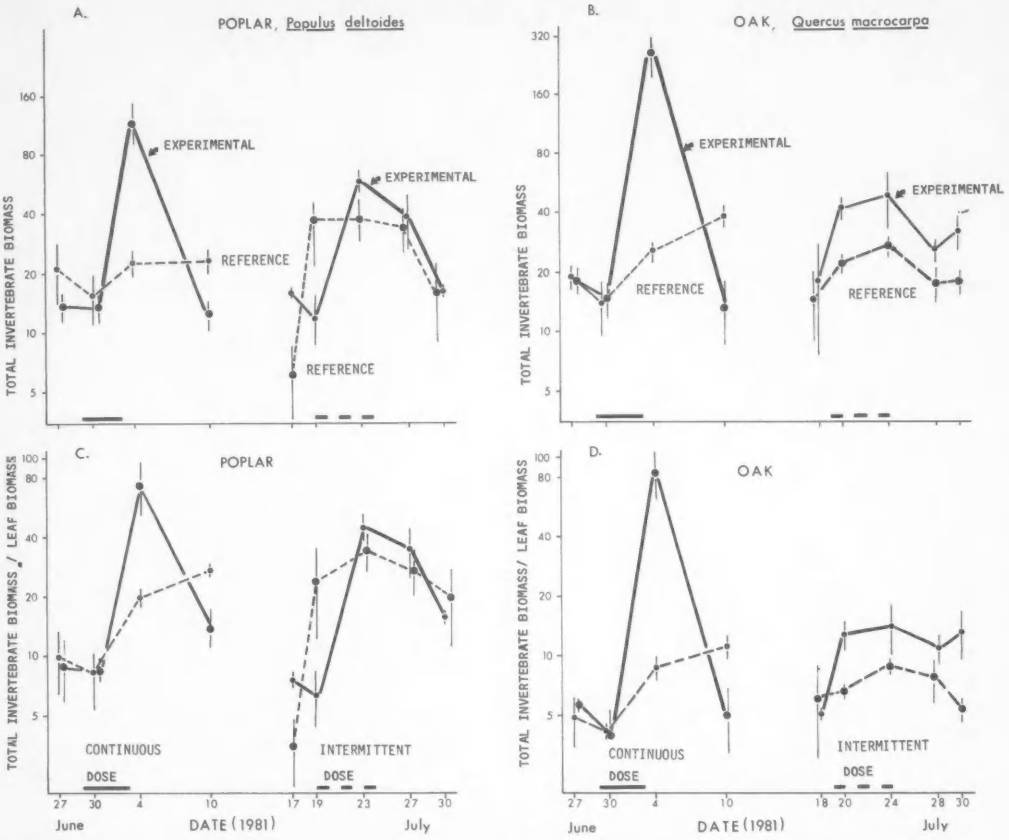

FIG. 5. Invertebrate biomass changes (mg) on leafpacks. Solid lines = experimental channels; broken lines = reference channels. Vertical bars = standard error about the mean. (A) Total invertebrate biomass on leafpacks of poplar; (B) Total invertebrate biomass of leafpacks of oak; (C) Total invertebrate biomass (mg) over total leafpack dry mass (mg) for poplar leaves; (D) Total invertebrate biomass (mg) over total leafpack dry mass (mg) for oak leaves.

midpoint of the first dose. After 48 h into the dose, snails were also found in high numbers in the sump pump where water was recirculated to the upper end of the channel. Apparently, snails release themselves from substrata and passively drift when disturbed. The low oxygen tension may have caused this response rather than the toxicant, as a similar phenomenon was not observed during the intermittent dose.

The numbers of flatworms on leafpacks were very high in experimental channels during both doses relative to the control channels. Possibly, damage or stress to other organisms triggered higher recruitment rates for these scavenger–predators.

Various species of insects colonized leaf packs; however, only the Diptera were found with any frequency. Numbers of chironomids tended to decrease in channels dosed with *p*-cresol, but their numbers were always so low that definitive conclusions cannot be drawn. No trend was found for the tanypodids.

INVERTEBRATE AND LEAF BIOMASS CHANGES OVER TIME

The biomass of invertebrates changed over time for both poplar and oak leaves (Fig. 5A and B). Invertebrate biomass increased significantly in the experimental channel during the continuous dose from 29 June to 3 July. The increase was caused by snails, isopods, leeches and flatworms colonizing leafpacks (see also Tables 3 and 4). Unlike leeches and isopods, snails and flatworms were usual components of the leafpack community; even so, their biomass increased substantially in the experimental as compared with the control channel. No differences in biomass values were observed between the experimental and reference channel for the intermittent dose.

The pattern remained unchanged when invertebrate biomass was adjusted for reductions in leaf dry mass over time (Fig. 5C and D). The values for invertebrates per unit dry mass of oak were lower than for poplar.

Discussion

Continuous dosing of *p*-cresol at 8 mg/L damaged the invertebrate aquatic community more than did intermittent dosings of the toxicant at the same concentration. We hypothesized that the indirect effect of *p*-cresol on the ecosystem, namely reductions in dissolved oxygen, contributed to the community changes. Based on laboratory data, we had expected only the scud to be seriously affected by 8 mg/L *p*-cresol. Yet, snails, flatworms, isopods, and leeches showed behavioral changes that were more pronounced during the continuous dose when dissolved oxygen fell to less than 1 mg/L for long periods. Increases in abundance of those species on leafpacks during doses could have been caused by individuals leaving usual habitats during oxygen depletions. Isopods normally inhabited root mats of emergent grasses and sedges. Only during the continuous dose were they found in any numbers on the leafpacks. Their low abundances on leaves during the intermittent dose and their higher resistance to *p*-cresol in the laboratory suggest that the low dissolved oxygen affected them more than the *p*-cresol.

Behavioral changes of individual invertebrate species permitted more insight into changes in community stability than did structural properties of the community because the structural indices do not distinguish one species from the other. Because a number of the invertebrate species in the system behaved uniquely in response to stress, tracking species in the community system is more useful, in most cases, in a community analysis than is examining fused structural community indices.

Species' responses to stress, when studied within a community framework rather than in a population framework, also allow theories describing interspecies interactions and genetic variability to be developed. These types of field studies can invalidate community-level predictions based on laboratory-derived data.

The loss of mass of poplar leafpacks fits the exponential decay model described by Short et al. (1980), although the k (or loss rate) was high relative to values reported in their paper. That is to be expected as the water temperature was much higher in Monticello channels. Benfield et al. (1977) found that the shredder community was unimportant in leaf processing for a pastureland stream, which normally received little in the way of leaf inputs. This was also true for the channels at Monticello.

Poplar leaves had significantly lower mass loss in the experimental channel during the 96-h continuous dose as compared with the reference channel and with the intermittent dose. A direct cause cannot be given. Several factors may be involved. Invertebrates may have been inhibited in their feeding owing to the combined effects of *p*-cresol and oxygen stress; direct chemical interference may have slowed degradational processing, and/or indirect interference with microbial processing may have occurred. With regard to the last point, . . Pritchard (EPA, Gulf Breeze Lab., FL) showed that under laboratory and field conditions, *p*-cresol-degrading bacteria ceased degrading *p*-cresol when the dissolved oxygen dropped below 0.8 mg/L. It is possible that aerobic bacteria associated with leaf processing were also inhibited by the low dissolved oxygen. Definitive experiments separating effects of invertebrate feeding, *p*-cresol and low dissolved oxygen are necessary before a principal cause can be postulated.

Acknowledgments

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Stable Carbon Isotope Ratios: Implications for the Source of Sediment Carbon and for Phytoplankton Carbon Assimilation in Lake Memphremagog, Quebec[1]

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LAZERTE, B. D. 1983. Stable carbon isotope ratios: implications for the source of sediment carbon and for phytoplankton carbon assimilation in Lake Memphremagog, Quebec. Can. J. Fish. Aquat. Sci. 40: 1658 – 1666.

The stable carbon isotope (SCI) ratio of the sediment of Lake Memphremagog, Quebec is compared with that of terrestrial sources and the phytoplankton to determine the relative proportion of allochthonous carbon incorporated into the sediments. Approximately 40–50% of the organic carbon in the main basins' pelagic sediment was terrestrial in origin, whereas up to 100% was terrestrial in littoral areas. The SCI method of determining the organic carbon source of sediments appears more reliable than the C/N method. A comparison of the SCI fractionation of the phytoplankton with laboratory cultures under different degrees of carbon limitation indicates that the phytoplankton of Lake Memphremagog are not carbon limited and fix carbon primarily by the C_3 pathway.

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Le rapport des isotopes de carbone stables (SCI) du sédiment du lac Memphremagog, au Québec, a été comparé avec celui de sources terrestres et le phytoplancton, en vue de déterminer la proportion relative de carbone allochtone incorporé dans le sédiment. Environ 40–50 % du carbone organique dans le sédiment pélagique des bassins principaux est d'origine terrestre, alors que dans les régions littorales, il peut être jusqu'à 100 % terrestre. La méthode des SCI pour déterminer la source de carbone organique du sédiment semble plus fiable que celle de C/N. Quand on compare le fractionnement des SCI du phytoplancton avec des cultures en laboratoire à différents degrés de limitation du carbone, on constate que le phytoplancton du lac Memphremagog n'est pas limité par le carbone et qu'il fixe cet élément principalement par la voie de C_3.

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THE organic matter of lacustrine sediments is potentially derived from at least two major sources: autochthonous contributions such as the phytoplankton and allochthonous (terrestrial) material. These different sources of carbon and their relative deposition rates are germane to the study of whole lake and watershed carbon cycles (Mackereth 1966) as well as to the study of the organic chemistry of the sediments themselves (e.g. Meyers et al. 1980; Cranwell 1974). The cycling of elements strongly associated with organic matter (e.g. some metals) is also more easily predicted if information on the relative composition of the sediments is available (Nriagu 1982).

In freshwater environments, the carbon to nitrogen ratio (C/N, in g/g) has been the primary indicator of sediment source (e.g. Nriagu 1982; Kemp et al. 1977). However, as will be illustrated later, this method has two drawbacks: one being the unambiguous determination of C/N of the two alternative sources and the other being the stability of this ratio during sediment diagenesis. Specific organic compounds, symptomatic of terrestrial or lacustrine sources, can also be used (Cranwell 1976) with similar reservations. In numerous studies on marine sediments, the different stable carbon isotope (SCI) ratios of the plankton versus fluvial loadings of terrestrial organic material has permitted the relative proportion of these two sources to be estimated (e.g. Northam et al. 1981; Nissenbaum and Kaplan 1972; Sackett and Thompson 1963). The difficulties encountered in the interpretation of C/N ratios do not appear to be as pronounced with SCI ratios (Northam et al. 1981; Nissenbaum and Kaplan 1972; Sackett and Thompson 1963; see also discussion).

For the SCI method to be useful in freshwaters, it is necessary that the phytoplankton maintain a significantly different

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SCI ratio from that of the terrestrial sources. Although there is some indication that this may generally occur (e.g. Rau 1978; Degens 1969), the only previous attempt to use this method failed because of the high variability of SCI ratio in the phytoplankton (Stiller 1976). However, this failure may have been the result of the lake's (Lake Kinneret, Israel) high pH and consequent $CaCO_3$ precipitation during peak phytoplankton blooms. These factors can lead to carbon limitation in the phytoplankton, a possible shift in carbon uptake pathway, and consequent reductions in SCI fractionation (see discussion).

The primary intent of this study was to use SCI ratios to ascertain the relative proportion of allochthonous versus autochthonous organic carbon in the sediments of Lake Memphremagog, Quebec, and to compare these estimates with those obtained from the C/N method. In addition, a detailed analysis of the SCI fractionation of the phytoplankton was obtained, which permitted some comparison with laboratory cultures under different degrees of inorganic carbon limitation and differing pathways of carbon fixation. Finally, the relevance of this study to the interpretation of the stable carbon isotope ratios of ancient sediments is assessed.

Methods

Phytoplankton samples were collected at four stations along the North–South axis of Lake Memphremagog, Quebec (Fig. 1; 2/, 5/, 7/, 9/) using a tube sampler which integrated over the epilimnion. Occasional microscopic examination of preserved samples revealed negligible detritus. The samples were acidified to pH 3 with dilute HCl and centrifuged at 250 × *g* for 10 min or more. The resulting pellet was dried at 70°C and ground before combustion.

Ten cores were collected with a gravity corer, a shallow water piston corer, or by SCUBA at different stations along the North–South axis of Lake Memphremagog (Fig. 1). Upon extrusion, they were sliced (usually at 18-mm intervals), dried at 70°C and ground. The larger wood fragments (>1 mm) were sifted from one littoral core (QL/10) before analysis of the residual material. Subsamples of the core sections were thoroughly washed with 1% sulfurous acid (Gibbs 1977) to remove any residual inorganic carbon, then redried and reground before combustion.

Precombusted CuO was added to the sample in a platinum boat before combustion at 900–1000°C in a pure oxygen atmosphere. The purified CO_2 gas was analyzed on a Vacuum Generators Micromass 602 ratiometric mass spectrometer with the usual corrections for ^{17}O, peak overlap and valve leakage applied (Hillaire-Marcel 1976). The results are reported relative to the PeeDee Belemnite limestone standard as:

$$\partial^{13}C(‰) = (((^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{pdb}) - 1) \times 1000.$$

Fractionation between organic carbon and its inorganic source carbon is reported as $\Delta^{13}C(‰) = \partial^{13}C(org) - \partial^{13}C(inorg)$. This is consistent with the usual use of the term (e.g. Calder and Parker 1973; Degens et al. 1968); but "fractionation" so defined is approximately the negative of "discrimination" as defined by O'Leary (1981) when considering the samples here.

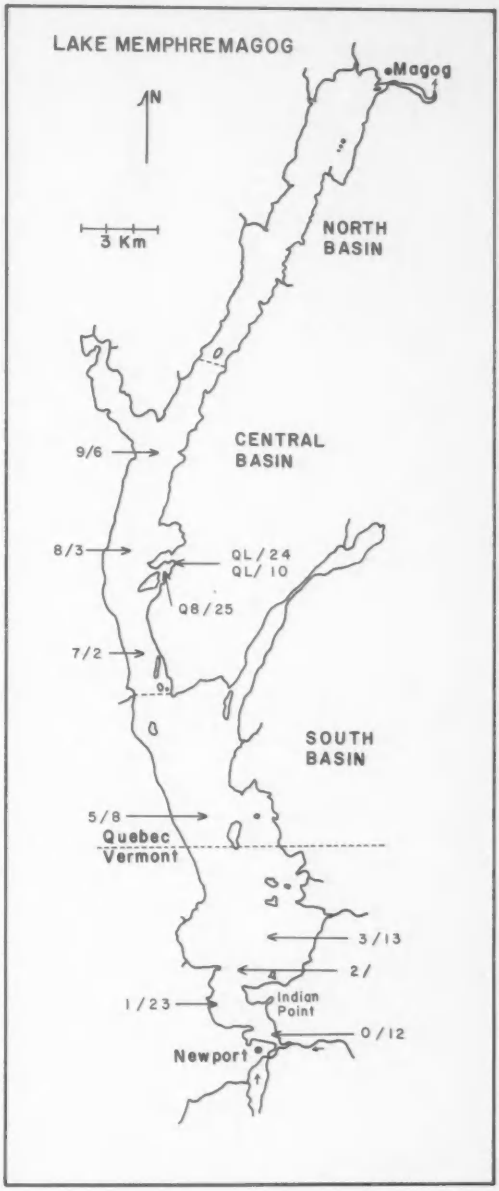

FIG. 1. Station locations (e.g. 2/ or 7/) and core identification numbers (e.g. /10 or /23) in combination for Lake Memphremagog, Quebec.

Humic and fulvic acids were extracted from sediments using the method of Nissenbaum and Kaplan (1972).

TABLE 1. Core depth (d; mm), stable carbon isotope ratio ($\partial^{13}C$; ‰), mean $\partial^{13}C$ ($\bar{x}$), standard deviation (SD), and percent terrestrial carbon (%).

(Station No.)/(Core No.)																	
0/12		1/23		3/13		5/8		7/2		8/3		9/6		Q8/25		QL/24		QL/10	
d	$\partial^{13}C$	d	$\partial^{13}C$	d	$\partial^{13}C$	d	$\partial^{13}C$	d	$\partial^{13}C$	d	$\partial^{13}C$	d	$\partial^{13}C$	d	$\partial^{13}C$	d	$\partial^{13}C$	d	$\partial^{13}C$
9	−28.2	9	−28.3	9	−30.3	9	−30.5	10	−29.6	13	−29.1	8	−29.1	9	−31.4	9	−27.2	9	−25.3
27	−28.2	27	−28.3	27	−30.8	27	−30.5	35	−30.3	40	−30.7	50	−30.5	45	−28.8	27	−27.2	45	−26.4
45	−28.2	45	−30.0	45	−30.4	45	−31.2	65	−29.7	70	−32.3	140	−28.6	99	−27.6	45	−27.5	99	−26.2
63	−27.3	63	−29.3	63	−30.7	63	−30.0	95	−30.7	103	−31.6	255	−28.2	171	−27.9	63	−26.3	171	−25.4
81	−28.2	81	−27.7	81	−30.7	81	−30.0	125	−30.5	138	−30.1			262	−27.4	81	−26.4	261	−25.9
117	−27.6	99	−26.7			117	−29.4	155	−29.8	173	−29.6					99	−26.1		
153	−27.1	135	−28.0			153	−30.9	185	−31.5	200	−30.4					117	−26.5		
189	−27.1	171	−27.8			189	−30.3	215	−28.9	234	−30.5					135	−26.6		
225	−27.9	207	−30.1			225	−29.3	245	−29.1	271	−30.3					153	−26.5		
261	−28.1	243	−28.0			261	−30.7	276	−28.7	305	−29.5					171	−26.4		
297	−28.4	279	−28.2			297	−29.3	302	−29.8	313	−29.2					207	−26.6		
333	−28.2	315	−30.3													243	−26.6		
		351	−28.3													279	−26.7		
																315	−26.7		
																351	−27.3		
																387	−26.7		
																423	−27.5		
																459	−26.9		
																495	−27.2		
$\bar{x}$	−27.9		−28.5		−30.6		−30.2		−29.9		−30.3		−29.1		−28.6		−26.8		−25.8
SD	0.5		1.1		0.2		0.7		0.8		1.0		1.0		1.7		0.4		0.5
%[a]	81[c]		69		40		42		43		35		51		71		88		103
%[b]	90		79		46		49		50		41		60		74		104		121

[a]Assumes −26‰ terrestrial; $\partial^{13}C$ of phytoplankton interpolated from adjacent stations.
[b]Assumes −27‰ terrestrial.
[c]Phytoplankton $\partial^{13}C$ for this station obtained by assuming a DIC of −10‰ (LaZerte and Szalados 1982) and a fractionation factor of −26‰ (see text).

TABLE 2. Phytoplankton $\partial^{13}C$ (‰) and chlorophyll-a (μg/L).

	Station							
	2		5		7		9	
14 May 79	−34.4	4.0	−33.7	4.4			−31.0	5.4
18 May	−34.2	5.8	−33.3	6.7			−33.1	6.0
31 May	−34.8	3.5	−33.6	4.8			−35.2	4.3
11 June	−34.9	2.8	−35.0	3.0			−33.7	2.5
21 June	−30.9	9.3	−32.5	7.8	−31.0	4.6	−29.9	3.5
26 June	−32.3	8.3	−31.6	6.6	−31.7	5.0	−28.7	3.5
5 July	−31.7	5.7	−30.6	3.5	−33.2	3.1	−29.3	2.5
16 July	−33.6	3.5	−30.1	2.0			−31.7	3.0
26 July	−34.7	8.9	−31.5	6.4	−32.5	5.4	−34.0	4.4
6 August	−34.7	5.0	−32.9	7.7			−33.4	3.6
16 August	−34.3	13.9	−34.6	10.0			−30.2	5.3
23 August	−36.0	18.4	−36.6	7.1			−35.5	5.4
Average[a]	−34.0		−33.2				−32.3	
$\Delta^{13}C$[b]	−25.9		−26.0				−25.6	

[a]Chlorophyll-a weighted seasonal average.
[b]Computed as the difference between the above average and the seasonal average DIC at the same station (fig. 2, LaZerte and Szalados 1982).

Phaeophytin-corrected chlorophyll-a was determined from 500 mL of the same water sample used for phytoplankton $\partial^{13}C$ analysis using a fluorometer calibrated against Strickland and Parsons' (1968) spectrophotometer method (Watson 1979). Total carbon and nitrogen in the sediment were analyzed by the Rexdale laboratory of the Ontario Ministry of the Environ-

ment using a LECO induction furnace carbon analyzer and the Kheldahl method for nitrogen (Anon. 1981).

Results

Based on the summary of Degens (1969) and measurements of the $\partial^{13}C$ of organic carbon in major rivers and river sediments (e.g. Stiller 1976; Salomons and Mook 1975; Sackett and Thompson 1963) the usual $\partial^{13}C$ estimate for terrestrially derived carbon is -25 to $-27‰$. The drainage basin of Lake Memphremagog is predominantly deciduous forest although pasture may have been more important in the past (J. Kalff, McGill Univ., Montreal, Quebec, personal communication). Direct inputs of organic carbon to the littoral enter primarily as wood and deciduous leaf litter. Leaf litter samples collected in 1979 were $-25.7 \pm 1.0‰$ (mean $\pm$ standard deviation, $n = 4$) and in 1982 were $-28.0 \pm 1.1‰$ ($n = 6$). These values are consistent with the usual average of $-26‰$. A value of $-27‰$, however, might be more representative of the leaf litter component of terrestrial inputs and $-26‰$ more representative of the wood component as leaf material can be $1-2‰$ lighter (more negative) than wood (Leavitt and Long 1982). A $-26‰$ for wood is also suggested by a comparison of the $\partial^{13}C$ value of the littoral core QL/10 with a visual inspection revealing the predominance of woody organic material (see below). For the purposes of this study, however, $-26‰$ will be taken as the SCI ratio for all forms of terrestrial organic carbon entering the lake.

Six of the 10 cores were initially examined in detail to determine if there were any changes in $\partial^{13}C$ with depth (Table 1; 0/12, 1/23, 5/8, 7/2, 8/3, QL/24). As the vertical profiles were very homogeneous, the remaining four cores were only analyzed at geometrically increasing depth intervals. Only one of these last four cores (Q8/25) may have a trend with depth. The core average $\partial^{13}C$ values follow a distinct pattern (Table 1); those from the main basins of Lake Memphremagog (3/13, 5/8, 7/2, 8/3, 9/6) have homogeneous and more negative values of $\partial^{13}C$ (overall mean of $-30.0 \pm 0.6‰$) than those closer to the southern river mouths (0/12, 1/23) or closer to or in the littoral (Q8/25, QL/24, QL/10). These last cores tend to be more positive the closer they are to the terrestrial source. In particular, the $\partial^{13}C$ of the two littoral cores (QL/10 and QL/24) cannot be distinguished from the earlier estimate of the $\partial^{13}C$ of terrestrial material ($-26‰$), and core 0/12 is very close to this estimate.

The phytoplankton of Lake Memphremagog have substantially more negative carbon ratios than the terrestrial material of the surrounding landscape (Table 2). At each station there is a possible trend toward more positive values from mid-June to early July during a diatom bloom dominated by *Asterionella formosa* and *Fragilaria crotonensis*. However, a more substantial late August bloom dominated by the colonial blue-green bacteria *Anabaena* sp. and *Coelosphaerium* sp. exhibited more negative $\partial^{13}C$ values. The annual chlorophyll-*a* weighted averages increase from a more negative $-34.0‰$ at the station closest to the incoming rivers (2/) to $-32.3‰$ at the station most distant (9/). The average fractionation of the phytoplankton with respect to the seasonal average dissolved inorganic carbon (DIC) $\partial^{13}C$ at each station (LaZerte and Szalados 1982) is $-25.8‰$. There is no trend in average fractionation down the axis of the lake as the average phytoplankton and DIC SCI ratios are linearly correlated ($R^2=0.96$) with a slope not significantly different from 1.0.

At the pH of Lake Memphremagog (7–8) almost all DIC is in the bicarbonate form and thus the fractionation with respect to CO_2(aq) can be directly computed using either Deuser and Degens' (1967) relationship:

$$\partial^{13}C\text{–}CO_2(aq) = -7.3 + \partial^{13}C\text{–}HCO_3^- \text{ at } 20°C$$

or using the more recent relationship of Mook et al. (1974):

$$\partial^{13}C\text{–}CO_2(aq) = -9.5 + \partial^{13}C\text{–}HCO_3^- \text{ at } 20°C.$$

In comparing the fractionations so obtained with other work, care should be taken to ascertain which of the above relationships is employed (and at which temperatures) as even the newer literature can employ the older relationship (e.g. LaZerte and Szalados 1982). Using Mook et al.'s relationship (1974) the average fractionation of the phytoplankton with respect to CO_2(aq) is $-16.3‰$.

Assuming that the mass of phytoplankton chlorophyll is reasonably correlated with the mass of phytoplankton carbon, the chlorophyll weighted averages of phytoplankton $\partial^{13}C$ should represent the $\partial^{13}C$ of the phytoplankton derived carbon incorporated into the sediments. Assuming also that $-26‰$ represents the terrestrial endmember and that there are no other significant carbon sources, these values can then be used to obtain the relative proportion of terrestrial versus phytoplankton carbon incorporated into the sediments of each core (Table 1). The mean percent terrestrial composition of the five cores representing the main basins is $42 \pm 6\%$ whereas the other cores (in particular, QL/10) approach 100% terrestrial material. Core QL/10 was dominated by wood fragments below 162 mm of organic muck. Even though the larger (>1 mm) fragments had been removed before $\partial^{13}C$ analysis, the residual organic material below 162 mm was most likely wood derived. This conclusion is verified by a high C/N ratio characteristic of woody tissue (see below). Thus the value of $-26‰$ for terrestrial SCI ratios appears well supported by this core. The sensitivity of this analysis to the choice of terrestrial SCI ratio is illustrated with the value of $-27‰$ (Table 1). As expected, the cores with the least apparent terrestrial component (the mid-basin cores) are least affected, whereas the littoral cores, in particular core QL/10, respond more dramatically.

The $\partial^{13}C$ of two humic acid and two fulvic acid samples from surface sediments in the vicinity of the two littoral cores were not significantly different from terrestrial carbon ($-26.1 \pm 1.2‰$).

Carbon and nitrogen could not necessarily be analyzed on the same core sections as were used for SCI ratios because of inadequate sample size; and, in particular, core 3/13 had insufficient organic matter for both analyses in all sections. The values obtained (Table 3) do exhibit more within core variability than found for the SCI ratio. This is especially pronounced in the littoral cores (QL/10, QL/24). Organic carbon levels are lower toward the southern river mouths (0/12, 1/23) and highest in the Quinn Bay area (Fig. 1;

TABLE 3. Core depth (d; mm), carbon (mg/g dry weight), C/N, means ($\bar{x}$), standard deviation (SD), and percent terrestrial carbon (%).

(Station No.)/(Core No.)																													
0/12			1/23			5/8			7/2			8/3			9/6			Q8/25			Q1/24			Q1/10		
d	C	C/N	d	C	C/N	d	C	C/N	d	C	C/N	d	C	C/N	d	C	C/N	d	C	C/N	d	C	C/N	d	C	C/N
9	41	10.0	9	25	10.0	9	52	8.4	10	59	7.8	13	54	8.4	8	53	8.2	9	86	9.1	9	81	14.2	9	69	10.5
27	39	10.3	27	22	10.5	27	52	7.5	35	57	8.5	40	51	13.4	15	60	8.5	27	90	11.4	27	79	11.6	27	73	11.8
99	40	11.8	99	21	10.5	45	51	8.6	155	49	8.3	173	47	8.7	50	54	8.6	99	88	14.0	153	96	18.8	99	65	13.8
207	47	20.4	207	25	10.9	99	41	10.3	302	49	10.2	313	50	10.4	140	52	8.4	207	91	18.2	207	150	29.4	207	84	35.0
333	37	13.7	351	66	27.5	207	27	9.6							273	51	9.4	351	91	17.2	351	57	13.9	351	40	25.0
$\bar{x}$	41	13.2		32	13.9		45	8.9		54	8.7		51	10.3		54	8.6		89	14.0		93	17.6		66	19.2
SD	4	4.3		19	7.6		11	1.1		5	1.1		3	2.3		4	0.5		2	3.8		35	7.1		16	10.5
%[a]		57			63			26			24			36			24			63			90			102
%[b]		47			53			8			6			21			5			54			86			100
%[c]		81			89			37			34			51			33			90			127			144

[a]Assumes phytoplankton C/N of 5.4 and terrestrial C/N of 19.
[b]Assumes phytoplankton C/N of 8.0 and terrestrial C/N of 19.
[c]Assumes phytoplankton C/N of 5.4 and terrestrial C/N of 15.

Q8/25, QL/24, QL/10). Nitrogen, although also low in the southern regions, exhibits no other pattern. The core average C/N values are higher in the Quinn Bay area and towards the southern river mouths. The high C/N values at depth in core QL/10 is associated with the dominance of wood fragments below the 162 mm muck layer. As with the $\partial^{13}C$ values, the core average C/N values of the main basin cores (5/8, 7/2, 8/3 and 9/6) are relatively uniform with an overall average of 9.1 ± 0.8. The core average pattern correlates well with the core average SCI ratio with an R^2 of 0.87 ($C/N = 80 + 2.4\ \partial^{13}C$). However when the available individual C/N values are matched with the $\partial^{13}C$ values of the same core section, the relationship is much less satisfactory ($R^2 = 0.23$); apparently the core averaging procedure eliminated much of the within core variation, particularly in the C/N values.

As with the use of SCI ratios, the use of C/N ratios to estimate the relative proportion of terrestrial carbon incorporated into sediments is only as accurate as the estimate of the endmember C/N ratios. One year (1975) of particulate carbon and nitrogen data in Lake Memphremagog is available from Carlson et al. (1979). The seasonal C/N average at individual stations varied from 4.85 to 6.11 with no apparent pattern down the length of the lake. Chlorophyll-*a* weighted averages are not available, but as there existed no difference between the C/N ratios at the highest and lowest productivity stations, they do not appear necessary. The grand average C/N is 5.38 ± 0.45 ($n = 8$). This is lower than that reported in Kemp et al. (1977) for Lake Ontario (6.3−7.8) but is not significantly different from the average C/N value for marine phytoplankton (5.9, Bordovskiy 1965; 5.5 to 7.5, Muller 1977). Nriagu (1982) reports an average value of 7.9 for soft water lakes of northern Ontario and a range of 6−8 for Lake Erie. Overall, a range of 5.4−8 appears justified.

Published terrestrial C/N values also vary, depending both on the original source and on its state of decomposition. The "critical" C/N value, above which little further nitrogen mineralization of the organic matter occurs, can vary from 15 to as high as 33 depending upon the material (Black 1967). The lower value also represents nitrogen sufficient, undecomposed terrestrial organic material (Salisbury and Ross 1967). As woody tissue can have nitrogen contents an order of magnitude less than fresh leaves (Woodwell et al. 1975), some additional ambiguity can occur. For example, core QL/10 has a uniform $\partial^{13}C$ profile but sharply increasing C/N values after the 162 mm muck layer was passed and the region dominated by wood fragments encountered. The occasional high C/N values encountered in QL/24 and the other cores closer to the littoral may also be the result of localized wood deposits. In contrast, the relatively uniform $\partial^{13}C$ profiles of these cores implies that there is little difference in the SCI ratio of terrestrial inputs (e.g. wood versus leaf litter), providing some additional justification for the choice of a single value (−26‰) for the SCI ratio of terrestrial input.

This difference in C/N value of the two major terrestrial sources (wood versus leaf litter) can cause substantial ambiguity in the prediction of source proportions. For example, the usual estimate of terrestrially derived C/N ranges from 15 to 20 (e.g. Nriagu 1982). Because of this high variability, I will first arbitrarily assume that an average C/N of 19 represents

terrestrial input. This will fix core QL/10 at approximately 100% terrestrial, the value obtained using the $\partial^{13}C$ method. Using 5.4 for the phytoplankton endmember (Table 3), the estimates of percent terrestrial composition depart markedly (from those derived with $\partial^{13}C$ values) in the main basin cores which have a low percentage of terrestrial carbon. If the value of 8 for phytoplankton C/N is used, an even greater discrepancy is observed, again at the low percent terrestrial end. Using a terrestrial C/N value of 15 removes most of the discrepancy in the main basin cores, but also gives anomalously high values, greater than 100%, for the littoral cores. By reversing the above procedure, the $\partial^{13}C$ estimates of percent terrestrial carbon in the main basins (42%) can be used to estimate the C/N ratio of the incoming terrestrial carbon as 14.2. These lower estimates of terrestrial C/N (14−15) obtained for the main basins are more characteristic of leaf litter than woody material.

Discussion

The Phytoplankton

Few estimates of the SCI ratio of freshwater phytoplankton exist. In general they tend to be more negative than terrestrial material (W. Salomons, Delft Hydraulics Lab., Haren, The Netherlands, personal communication; Salomons and Mook 1981; Rau 1978; Stiller 1976; Degens 1969) probably because of the more negative $\partial^{13}C$ of their source carbon. The dissolved inorganic carbon (DIC) in freshwater is generally out of isotopic equilibrium with the atmospheric CO_2 and lighter (more negative) because of the substantial influence of DIC derived directly from organic material (e.g. LaZerte and Szalados 1982; Rau 1978; Mook 1970).

The high correlation between the DIC and phytoplankton $\partial^{13}C$ in Lake Memphremagog implies that the phytoplankton organic carbon is derived from local DIC at the same station, rather than having been transported from the more productive southern end of the lake (Ross and Kalff 1975) to the less productive central basin. Apparently the rate of recycling of the phytoplankton carbon is sufficiently greater than the mixing time between stations to allow this constant fractionation to be achieved.

The average phytoplankton fractionation with respect to CO_2(aq) of −16.3‰ observed in this study is almost identical to that reported by Degens et al. (1968) for the CO_2-cell fractionation of several marine unicellular diatoms under excess CO_2 conditions (about −16.5‰ when recomputed using the CO_2(aq)-HCO_3^- relationship of Mook et al. 1974). Pardue et al. (1976) obtained the maximum average fractionation of −21‰ (with respect to CO_2(aq), using the relationship of Mook et al. 1974) for four marine unicellular blue-green bacteria and a freshwater *Chlorella* sp. under excess CO_2 conditions. However, for three colonial blue-green bacteria, maximum average fractionations of only −15‰ with respect to CO_2(aq) were obtained.

All of the above researchers obtained lower fractionations at lower CO_2 levels, but an exact relationship with growth rate or carbon uptake rate is often difficult to define (e.g. Calder and Parker 1973). Lowered culture agitation rates also decrease fractionation (Degens et al. 1968). The usual explanation for these results is that increased diffusion resistance under CO_2-limiting conditions reduces the extent to which enzymatic fractionation in the carbon fixation step is expressed (see below and LaZerte and Szalados 1982; Smith and Walker 1982; O'Leary 1981; Deuser 1970; Degens et al. 1968). Increased diffusion resistance has also been invoked by Pardue et al. (1976) to explain the difference in maximum fractionation between unicellular and colonial blue-green bacteria.

However, for the relatively low maximum fractionation of the diatoms, an alternative explanation is their propensity for C_4 metabolism via phosphoenolpyruvate carboxylase (PEPCase; Kremer 1981; Beardall et al. 1976). In vitro, PEPCase only slightly fractionates carbon: about −2‰ with respect to bicarbonate (its substrate), or +7‰ with respect to CO_2(aq) assuming isotopic equilibrium between bicarbonate and CO_2(aq) which is perhaps justified by the ubiquitous presence of carbonic anhydrase in the phytoplankton (O'Leary 1981). Diffusion resistance will only decrease the expression of this already low fractionation and thus the much higher fractionation observed in the diatoms of Lake Memphremagog and the CO_2 saturated diatoms of Degens et al. (1968) indicate that they are not primarily fixing carbon by the C_4 pathway. Other evidence (along with the much greater fractionation factor, i.e. −30 ± 10‰, O'Leary 1981) suggests that C_3 metabolism with ribulose bisphosphate carboxylase dominates in other groups of the phytoplankton as well (Coleman and Colman 1981; Feuillade and Feuillade 1981; Kremer 1981; Raven 1980). Nonetheless, a partial fixation of carbon via the C_4 pathway in unicellular diatoms could explain their lower fractionation at CO_2 saturation (Degens et al. 1968) relative to unicellular green and blue-green algae (Pardue et al. 1976).

Bicarbonate uptake into an internal DIC pool, "a CO_2 concentrating mechanism" (Badger et al. 1980; Kaplan et al. 1980; Raven 1980; Steeman-Nielson 1966) does not complicate the analysis, assuming that the active uptake of bicarbonate does not fractionate in itself. The isotopic effect of this process would be the result of reduced diffusion resistance to DIC both internal (e.g. plasmalemma resistance) and external to the cell; fractionation would be increased. In practice, bicarbonate uptake may be associated primarily with CO_2 limitation under alkaline conditions and thus correlate more with low fractionations even though its immediate effect would be to increase fractionation somewhat by reducing the high carbon diffusion resistance.

As the dominant members of the Lake Memphremagog phytoplankton were either diatoms or colonial blue-green bacteria, and their average observed fractionation agrees well with that found in laboratory culture of similar organisms under CO_2 saturating conditions (Pardue et al. 1976; Degens et al. 1968), the simplest interpretation is that the Lake Memphremagog phytoplankton are also CO_2 saturated which implies negligible DIC diffusional limitation, at least in the external environment. This is in distinct contrast with the results obtained for the macrophytes of this lake (LaZerte and Szalados 1982), but agrees with other evidence suggesting that phosphorus, and not DIC, is limiting phytoplankton production in most lakes (e.g. Schindler 1974) and in Lake Memphremagog in particular (Carlson et al. 1979; Sproule and Kalff 1978).

THE SEDIMENT

As the $\partial^{13}C$ values of the cores exhibit little trend with core depth (up to 50 cm), the SCI ratio and the relative proportions of the two major carbon sources have probably not changed appreciably over the time span covered by the cores (approximately 350 yr for a 26 cm core; B. Flett, Flett Research Ltd., Winnipeg, Manitoba, personal communication). This lends some support to the use of a single year's average as an estimate of the phytoplankton endmember's $\partial^{13}C$ value. In addition, the cores provide no evidence for long-term modification of the SCI ratio in freshwater sediments, in agreement with results from ocean sediments (e.g. Sackett 1964) and terrestrial soils (e.g. Nissenbaum and Schallinger 1974).

Both methods of estimating the percent terrestrial composition ($\partial^{13}C$ and C/N) rely on a good estimate of the two endmembers. This appears to be best obtained with the $\partial^{13}C$ method, as any potential difference between leaf and woody terrestrial inputs is relatively small and there is less evidence for decompositional alteration of the ratio. This is particularly apparent when comparing the uniform $\partial^{13}C$ with the variable C/N values of the littoral cores. Because of the difficulty in estimating the C/N terrestrial endmember ratio, the respective estimates of percent terrestrial composition can differ between the two methods despite the fact that the core average C/N and $\partial^{13}C$ values are well correlated. In general, however, a good correlation between C/N and $\partial^{13}C$ does not always hold apparently because of the relative lability of nitrogen relative to carbon (Nissenbaum and Kaplan 1972).

It is probable that the terrestrial organic matter deposited in the main basins of Lake Memphremagog is derived more from leaf material than that deposited in shoreline environments where large woody fragments can dominate (e.g. core QL/10). As there can be substantial differences between these two sources in C/N ratio, the earlier difficulties in trying to use a single C/N value for the terrestrial end-member of both pelagic and littoral sites can be explained. Most likely the estimate of a terrestrial C/N of 14.2 for the main basin cores (using $\partial^{13}C$ data) versus 19 for the littoral site is the best approximation available. These values are not unreasonable given the usual 15–20 range (e.g. Nriagu 1982).

There is also the possibility of a third source of carbon in the littoral zone, as cores QL/10 and QL/24 were taken from a large macrophyte bed in Quinn Bay, and it is known that these macrophytes have more positive $\partial^{13}C$ values (an average of −17.5‰, LaZerte and Szalados 1982) than either the phytoplankton or terrestrial material. However, as the $\partial^{13}C$ of these cores could not be distinguished from that of terrestrial carbon and there was visual evidence of a woody terrestrial source material dominating these cores, it can be concluded that macrophytes do not significantly contribute to sediment carbon (LaZerte and Szalados 1982). The breaking and long-range dispersal of these buoyant plants (primarily *Myriophyllum spicatum* and *Vallisneria americana*) may be one reason why they do not contribute, especially in the rather open wind-exposed embayment studied here; but also, in contrast to terrestrial plants, macrophytes contain little or no lignin-like material resistant to degradation (Hutchinson 1975).

As a result of the phytoplankton contribution, the SCI ratios of the main basin cores of Lake Memphremagog are more negative than might be expected in freshwater sediments. Lakes with plankton stable carbon isotope ratios even more negative than Lake Memphremagog do exist (Rau 1978), and we might expect to find sediments with even more negative SCI ratios accumulating as a result. Two preconditions might be a water mass strongly loaded with respired CO_2 (more negative) and a relatively high phytoplankton to terrestrial carbon ratio in the sediments. More eutrophic lakes would be likely candidates. This is of particular relevance in the interpretation of some ancient organic carbon deposits. Other interpretations of very negative $\partial^{13}C$ values in ancient sediments have been put forward (Schoell and Wellmer 1981) and could explain more extreme conditions.

The research presented here has shown that SCI ratios are a useful tool in the study of organic carbon deposition processes in various regions of a single lake and thus probably between lakes. Cranwell (1977), using specific organic compounds, has shown that the pelagic sediments of eutrophic lakes contain more autochthonous carbon than does the sediment of oligotrophic lakes. This proposed relationship could be tested quantitatively using the SCI method. A value of 40–50% terrestrial carbon in the sediments of mesotrophic lakes (as found here for mesotrophic Lake Memphremagog; Ross and Kalff 1975) may be quite common. The potential complexity of littoral sediments also deserves further attention, as I do not expect all macrophyte beds to have as negligible a macrophyte contribution to sediment carbon as shown by the one studied here, nor would I expect terrestrial, especially woody inputs to necessarily dominate at other littoral sites. Because of this potential variety in organic carbon composition and SCI ratios, a comprehensive study on pore water SCI ratios could reveal a greater diversity in relationships than that obtained at a single site (LaZerte 1981). The proposed explanations for the SCI fractionation of natural populations of phytoplankton, based on comparisons with laboratory cultures, are necessarily tentative given the paucity of data available. They should, however, provide a hypothetical framework for further research.

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Growth of Tagged American Lobsters, *Homarus americanus*, in the Bay of Fundy

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Sphyrion-tagged lobsters recaptured in the Bay of Fundy during 1977–80 yielded mean annual molt increment and molt probability data for male and female lobsters of 60–171 mm carapace length from which growth curves were calculated. In addition, a multiple regression model was used to generate growth curves from premolt size, number of molt periods lobsters were exposed to, and growth increment data for 850 tagged lobsters at liberty for 1–5 yr. Von Bertalanffy parameters were calculated from these empirical growth curves, which suggest that lobsters take 20–35 yr from time of hatching to reach 200 mm carapace length in the Bay of Fundy. Analysis of pleopods indicated that the majority of lobsters molt during August–October each year. Growth per molt of immature (60–94 mm carapace length) and mature (95–170 mm carapace length) male and immature female lobsters was arithmetic (regression slope 1.04) but was regressive for mature females (slope 0.95). Mature lobsters molted less frequently than immature lobsters, but mature males grew more rapidly than mature females. Most mature females in the Bay of Fundy are on a 2-yr molt–reproductive cycle. About 20% of ovigerous females recaptured within 2 yr after release had extruded eggs a second time without molting, confirming that multiple egg extrusions between molts do occur naturally.

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Des homards marqués au sphyrion et recapturés dans la baie de Fundy entre 1977 et 1980 ont montré des augmentations annuelles moyennes par mue et fourni des données sur la probabilité de mue de homards mâles et femelles de 60–171 mm de longueur de carapace (*L*) à partir desquelles on a calculé des courbes de croissance. De plus, on a utilisé un modèle de régression multiple pour obtenir des courbes de croissance à partir de la taille d'avant-mue, du nombre de périodes de mues auxquelles les homards ont été exposés et de données sur les augmentations de taille de 850 homards marqués et en liberté entre 1 et 5 ans. Des paramètres de von Bertalanffy ont été calculés à partir de ces courbes de croissance empiriques, et ces calculs donnent à penser qu'il faut de 20 à 35 ans après l'éclosion pour que les homards de la baie de Fundy atteignent 200 mm de longueur de carapace. On constate, à l'analyse des pléopodes, que la majorité des sujets muent entre août et octobre chaque année. La croissance par mue de mâles immatures (60–94 mm *L*) et matures (95–170 mm *L*), et de femelles immatures est arithmétique (pente de la régression 1,04), mais, dans le cas des femelles matures, elle est régressive (pente 0,95). Les homards matures muent moins fréquemment que les immatures, mais les mâles matures croissent plus rapidement que les femelles matures. La plupart de ces dernières dans la baie de Fundy ont un cycle de mue/reproduction de 2 ans. Environ 20 % des femelles ovigères et capturées moins de 2 ans après la mise en liberté avaient expulsé des oeufs une deuxième fois sans qu'il y ait mue, confirmant ainsi que plusieurs extrusions d'oeufs entre mues se produisent naturellement.

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KNOWLEDGE of growth rates is essential for understanding the population dynamics of a species. Estimation of crustacean growth rates under field conditions is complicated because all features that can be used to age an individual are lost during a molt. Approaches for determining lobster (Decapoda: Nephropidae) growth rates that circumvent this problem have included (1) polymodal analysis of length frequency data (Cassie 1954; Thomas 1973; Conan 1975a, 1975b), (2) application of molt data from tagging studies to the Ford (1933), Walford (1946), and Fabens (1965) methods for estimating parameters of the von Bertalanffy growth curve (Hepper 1967; Gibson 1969; Russell 1980), and (3) combining molt increment and molt frequency data, which are estimated separately (Kurata 1962; Ennis 1972, 1978, 1980;

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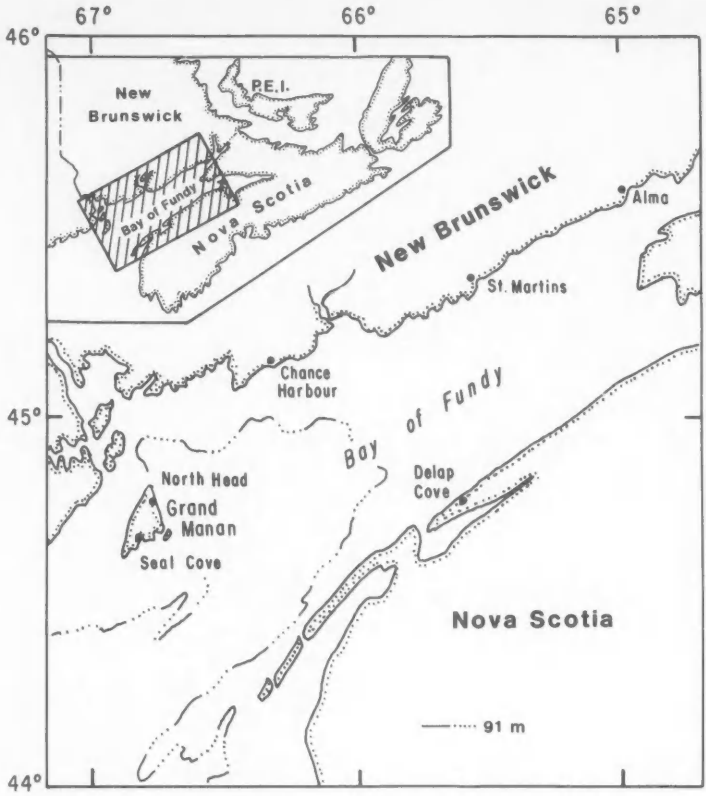

FIG. 1. Bay of Fundy showing fishing ports and adjacent areas where tagged lobsters were released.

Mauchline 1976, 1977; Cooper and Uzmann 1977; Fogarty et al. 1982). The third approach is probably the most realistic for estimating lobster growth in the field (Caddy 1977; Aiken 1980; Ennis 1980). Molt increments are obtained from tag release–recapture data and molt frequencies are estimated by means of shell condition sampling following the molting period (Ennis 1978) or by the "anniversary method" (Hancock and Edwards 1967), which estimates the proportion molting in a tagged size group 1 yr later. Ideally, in a field study of lobster growth, a sufficient number of the full-size range of lobsters should be tagged and released prior to and recaptured within a year after the beginning of the molting period to obtain annual growth increments and molt frequencies. However, with the infrequent capture and slow growth of large American lobsters, *Homarus americanus* (>105 mm carapace length, *L*), the use of data from tagged lobsters at liberty >1 yr is required. Conan and Gundersen (1979) successfully used data from tagged *Homarus gammarus* that had been at liberty up to 2 yr to calculate growth curves. Apart from this latter study, there is no information or methods for dealing with growth data from tagged American lobsters recovered >2 yr from the time of release.

There are few field studies of *H. americanus* growth in the Bay of Fundy (Fig. 1) and no published data on the growth of large lobsters (>105 mm *L*) in the Canadian Maritimes. Wilder (1953) reported on the growth of lobsters marked during 1947 and 1950 in Seal Cove, Grand Manan, but these data are restricted to immature lobsters (71.5–87.4 mm *L*). Templeman (1936) reported on growth of a few lobsters in a semiwild state (from lobster pounds) in Grand Manan.

In this study, average annual molt increment and molt probability data are presented for tagged lobsters in the 60–171 mm *L* range recaptured in the Bay of Fundy during 1977–80. Growth increment data for lobsters (60–175 mm *L*) at liberty 1–5 yr are analyzed using a new method of incorporating growth increment, time at large, and release size into a multiple regression model to predict growth rates of male and female lobsters. Growth rates of tagged lobsters from the Bay of Fundy are compared with published growth data of *H. americanus* from other areas.

Materials and Methods

Lobsters were caught in baited traps by professional fishermen off Grand Manan during 1978 and 1980 and off Chance Harbour and Alma, N.B. (Fig. 1), during 1979–80. The distal quarter of a pleopod endopodite of each lobster was removed with scissors and placed in a vial containing seawater cooled in ice. The pleopods were grouped in vials according to 5 mm L classes, transported to the laboratory, and held at about 2°C for <12 h prior to molt staging. With known bottom water temperatures, the approximate time of molting can be predicted from pleopod staging (Aiken 1973). Monthly bottom temperatures were obtained from PRINCE Station No. 5 near Grand Manan and from thermographs placed in 5–10 m of water off Chance Harbour and Alma during the summers of 1979–80.

Each lobster was tagged with a "sphyrion" spaghetti tag (Scarratt and Elson 1965), which is usually retained through ecdysis. The tag anchor was inserted into the dorsal musculature between the carapace and abdomen. Tagged lobsters were usually returned to the water as close as possible to the capture site less than 10 min after being removed from the traps. Information recorded for each tagged lobster included carapace length (L), sex, tag number, location, depth, and date of capture. The carapace length, from the base of the eye socket to the posterior margin of the carapace parallel to the mid-dorsal line, was measured with a vernier caliper to the nearest millimetre. The difference in measurements of L by various field personnel varied <1.5 mm.

Over 20 000 male and female lobsters of 60–203 mm L were tagged and released in the Bay of Fundy for growth and movement studies during 1977–80: Grand Manan during July–September 1977–78 (N = 5043), North Head (Grand Manan) during November–December 1977 (ovigerous females only, N = 457), Chance Harbour during July–September 1979–80 (N = 8058), St. Martins during July–August 1979 (N = 1257), Alma during August–September 1979–80 (N = 4801), and Delap Cove during August 1979 (N = 574) (Fig. 1). All recaptures were made by local commercial fishermen during subsequent fishing seasons. The fishermen were given a reward for returning tagged lobsters with information on date, location, and depth of recapture; L was measured by trained fisheries personnel. Only undamaged lobsters with all appendages intact were used for the growth study.

A predictive linear regression (Ricker 1973) was used to fit premolt (L_x) and postmolt (L_{x+1}) carapace length (millimetres) data:

$$(1)\quad L_{x+1} = a + bL_x$$

where a and b are regression coefficients estimated by the least squares method and x is an arbitrary intermolt number (Hiatt 1948). All lobsters released and recaptured between July 15 of one year and June 30 of the next year that had with certainty demonstrated growth, i.e. >4 mm, were analyzed for annual growth per molt. The majority of lobsters of >60 mm L were assumed to have the opportunity of molting no more than once per year in the Bay of Fundy (Wilder 1953; cf. this paper).

Interpretation of the premolt–postmolt data should be made with caution because two experimental sources of bias may occur. The first may be due to tag loss during molting and/or mortality due to poor application of tags so that average size-specific growth increment data may be biased downward. Individuals applying tags to lobsters were well trained and experienced so that tag loss was considered to be minimal (see also Cooper 1970). The second may occur due to lobsters molting without a detectable size increase, and in this paper, the exclusion of 0–4 mm L may bias the premolt–postmolt regression line upward. However, under field conditions, *H. americanus* molts without size increases are probably rare.

Premolt–postmolt regression lines for each sex, release location, and year were tested for statistical differences. Postmolt lengths were adjusted and tested for differences by analysis of covariance using premolt lengths as covariates (Snedecor and Cochran 1967). This is equivalent to comparing intercepts of the lines assuming lines have similar slopes and residual variances. As there were no significant differences ($P > 0.05$) between adjusted postmolt lengths and between slopes of the regressions of different areas and years, the data from all areas and years were combined to represent male and female premolt–postmolt growth for the whole of the Bay of Fundy. Previous information also indicates that lobster growth at molt from different areas varies little from year to year (Ennis 1972, 1978; Conan 1978). A computer program HIATT (Somerton 1980) was used to determine if there was an intersection point sufficient to indicate changes in growth increment at size at sexual maturity by determining if a pair of straight lines fitted the premolt–postmolt data significantly better than a single straight line.

The probability of annual molting was estimated from a modification of the "anniversary method" (Hancock and Edwards 1967), using data from lobsters that had had the opportunity of molting during the first molt period after release and were recaptured prior to the succeeding molt period. The molt period was considered to be August–October (see results on pleopod analysis, Table 1). Lobsters released off St. Martins, Chance Harbour, and Grand Manan prior to August 8 and recaptured after October 30 of one year and up to June 30 of the following year were considered for analysis of the proportion molting. As there were insufficient data to represent each release area adequately, the data were combined to represent the average for the whole of the Bay of Fundy during 1978–80. The relationship between annual probability of molting (P_x) and premolt size (L_x) for each 10 mm L group was fitted with an exponential curve:

$$(2)\quad P_x = ae^{bL_x}$$

where a and b are constants estimated by the least squares method. Mean annual growth (ΔL_x) was calculated as the product of molt increment and annual molt probability, $\Delta L_x = (L_{x+1} - L_x)P_x$.

A second method was used to estimate mean annual growth by relating growth increment to L at release and the time at liberty with the following multiple regression equation:

$$(3)\quad \Delta L_M = a + bM + cL_x + d\mu$$

where ΔL_M is the mean growth increment (millimetres) for

TABLE 1. Percentage of pleopod stages of lobsters in samples from Alma and Chance Harbour, 1979, and Grand Manan, 1978. Pleopod stages 3.0–3.5 and 4.0–5.5 indicate lobsters probably molting between 3–6 wk and 0.5–3.0 wk, respectively, at 10–15°C (Aiken 1973). Prediction of molting time for pleopod stage 1.0–2.5 is unreliable but usually exceeds 5 wk at 15°C.

		% of lobsters				
Area	Pleopod stage	July 16–31	August 1–15	August 16–31	September 1–15	November–December
Alma	0–2.5	76.7	54.3	84.2	90.0	100.0
	3.0–3.5	18.6	26.5	7.5	10.0	0
	4.0–5.5	4.6	19.2	8.3	0	0
N		129	151	120	20	80
Temperature (°C)		11.0	13.0	15.0	15.0	9.8
Chance Harbour	0–2.5	98.5	81.6	75.7	94.8	100.0
	3.0–3.5	1.0	14.0	18.5	2.6	0
	4.0–5.5	0.5	4.4	5.8	2.6	0
N		205	136	243	39	70
Temperature (°C)		10.0	11.0	11.0	11.5	10.0
Grand Manan	0–2.5	90.2	89.8	77.1	62.5	100.0
	3.0–3.5	9.8	8.6	21.6	6.3	0
	4.0–5.5	0	1.6	1.3	31.3	0
N		234	384	454	32	48
Temperature (°C)		10.0	11.0	11.7	11.0	8.0

lobsters of premolt release size L_x at liberty over M molt periods, μ is an interactive variable being the product of M and L_x, and a, b, c, and d are constants estimated with a multiple regression program (Kim and Kohout 1975). Lobsters at liberty 1–5 molt-years that had had a chance to molt during each annual molt period (July–October) were included in the multiple regression. In this study, for the size group considered, one molt period was assumed to offer 1 yr of potential growth. Growth curves were calculated for the second and third molt periods (years) with increasing size from the multiple regression for each sex.

Average von Bertalanffy growth curves for male and female lobsters were fitted to data points of size at age generated by the above two methods:

$$(4)\quad l_t = L_\infty (1 - e^{k(t-t_0)})$$

where t = age in years, l_t = carapace length at t, L_∞ = theoretical maximum L, k = constant, determining rate of increase or decrease in length increments, and t_0 = hypothetical age at which the organism would have been at zero length, using the method of Allen (1967).

Although the age of individual lobsters was not known, an estimate of the average age of lobsters at 81 mm L, for the purpose of calculating the von Bertalanffy growth parameters, was arbitrarily assumed at 6 yr for both males and females (see Aiken 1980). Only portions of growth curves for which data were available, e.g. within the 65–175 mm L range, were used to estimate the von Bertalanffy growth parameters.

Results and Discussion

MOLT PERIODS

Pleopod samples from lobsters caught in the Bay of Fundy during 1978–79 indicated that, of those molting, both sexes (60–150 mm L) would have molted during mid-August to late October (Table 1). Bottom water temperatures, which affect the timing of molt activity (Templeman 1936), did not exceed 12°C at Grand Manan and Chance Harbour and 15°C at Alma during the summer (Table 1). Lobsters with pleopod stages 3.0–3.5 would probably molt 3–6 wk after the samples were taken (Aiken 1973). The highest percentage of pleopod stages 3.0–3.5 occurred during the last 2 wk of August at Chance Harbour and Grand Manan but 1–2 wk earlier at Alma (Table 1). Percentages of pleopod stages 4.0–5.5, indicating molting would probably occur 0.5–3.0 wk after sampling, were highest in the first 2 wk of August at Alma, the last 2 wk of August at Chance Harbour, and the first 2 wk of September at Grand Manan. Lobsters with pleopod stages 1.0–2.5 sampled during July–September might have molted 1.5–3.0 mo later at 10–15°C, but because this was not possible to predict (Aiken 1973), the data were grouped with pleopod stage 0, which was considered the intermolt stage. Pleopod samples taken during January, March, and May 1980 from lobsters in three areas were all in the intermolt stage 0. Examination of over 500 lobsters each from Alma, Chance Harbour, and Grand Manan each year during mid-November 1976–81 revealed no soft-shelled lobsters, indicating no recent molting in all areas. In shallow waters such as at the head of the Bay of Fundy (e.g. Alma), higher temperatures during July–September may cause lobsters to molt earlier than in areas with cooler water towards the mouth of the bay (e.g. Chance Harbour and Grand Manan). These results are in agreement with those of others who have observed lobster molting at Grand Manan (Templeman 1936; Wilder 1953) and along the Maine coastline (Krouse 1973; Thomas 1973) during July–November, with the majority of molting in August–October.

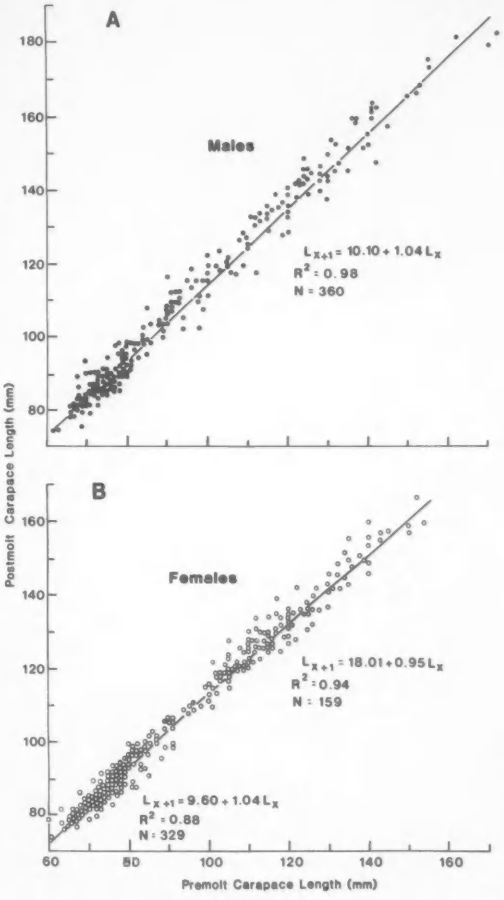

FIG. 2. Premolt (L_x)−postmolt (L_{x+1}) carapace length for tagged (A) male and (B) female lobsters showing growth within 1 yr of release in the Bay of Fundy, 1977−80.

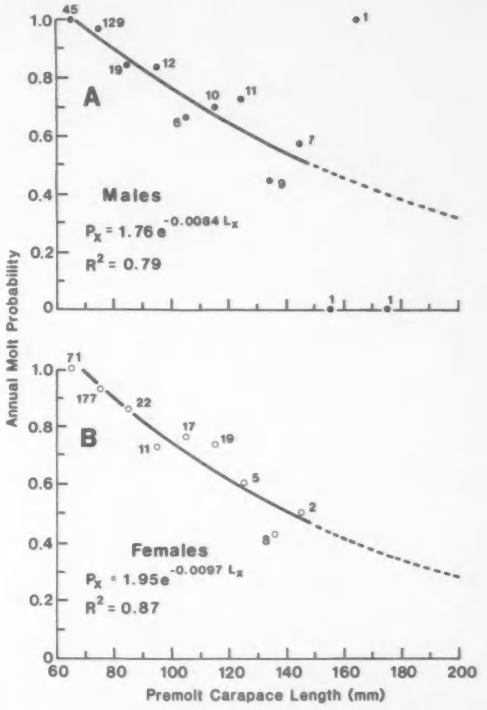

FIG. 3. Annual probability of molting (P_x) in relation to premolt carapace length (L_x) for (A) male and (B) female lobsters in the Bay of Fundy. Number of observations used to calculate each proportion shown by each data point. Broken lines are extrapolated beyond available data. Values with less than two observations were not used in regressions.

TAG RETURNS

By October 1, 1982, of the 4434 recaptured lobsters (22% of total releases), only about 25% were measured and could be considered for the growth analyses. Most tagged lobsters were recaptured only once because they were part of the commercial catch and were not returned to the water. A few multiple recaptures resulted from fishermen bringing tagged ovigerous females to the field observer for measurement and release.

GROWTH PER MOLT

Immature and mature premolt−postmolt regressions fit the data for females significantly better ($P < 0.01$) than a single straight line but not for males ($0.03 > P > 0.01$) using the Somerton (1980) method. As there was not a clear intersection point for males, the data for all sizes were included in a single regression (Fig. 2A). For females, the best fitting pair of straight lines was for an intersection point at a premolt L of 93 mm, which corresponds to a postmolt L of about 107 mm (Fig. 2B). This is similar to the medium size (108 mm L) of sexual maturity of females collected in the Bay of Fundy (Campbell and Robinson 1983) based on the pleopod examination technique (Aiken and Waddy 1982). A comparison of premolt−postmolt regressions between males and females of comparable size groups of immature (60−94 mm L) and mature (95−170 mm L) (all release areas and dates combined) was made using analysis of covariance. There were no significant differences ($P > 0.05$) in slopes and adjusted postmolt lengths between immature males and females, but there were highly significant differences ($P < 0.01$) in slopes and adjusted postmolt lengths between mature males and females. Correlations of all the premolt−postmolt regressions were significant ($P < 0.01$) (Fig. 2).

Growth per molt for both immature males and females

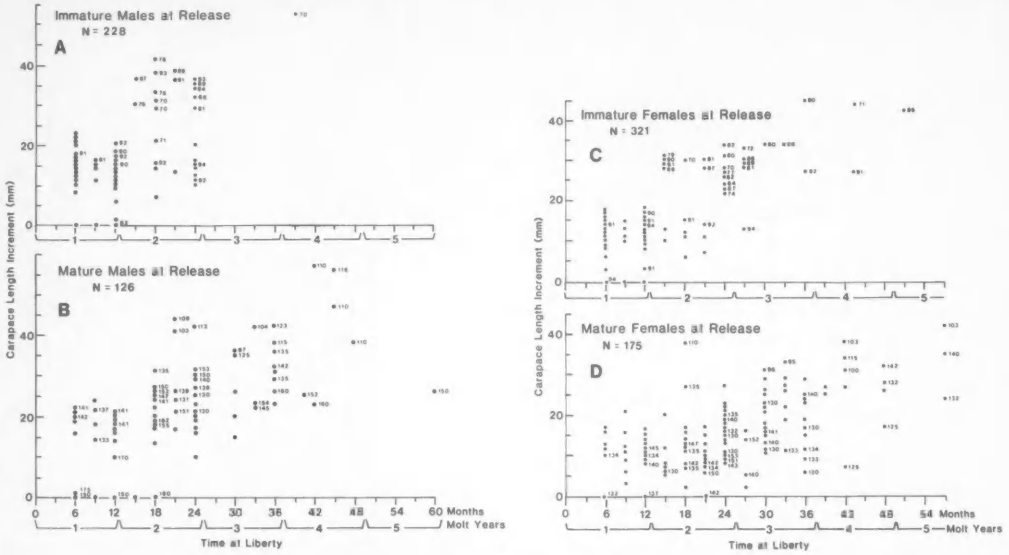

FIG. 4. Increment in carapace length (L) of recaptured tagged lobsters at liberty 3−57 mo or exposed to 1−5 molt periods (years) for (A) immature (60−94 mm L) males, (B) mature (95−175 mm L) males, (C) immature females, and (D) mature females when released in the Bay of Fundy. Data grouped for every 3 mo at liberty. Values beside each dot represent the release L in millimetres of large immature lobsters ≥90 mm L and/or with larger (>20-mm) increments and large mature lobsters ≥130 mm L and/or with larger (>35-mm) increments. Dots without values are for smaller lobsters and increments.

and mature males (Fig. 2) was arithmetic (b not significantly different than 1, $P > 0.05$, using t-test) (Draper and Smith 1966, p. 19) but tended towards being progressive ($b \geq 1.05$), whereas mature female growth was regressive (b significantly lower than 1, $P < 0.01$) (Kurata 1962). The results are similar to those reported elsewhere (Ennis 1972; Conan 1978; Aiken 1980). Although data reported in the literature show differences in premolt−postmolt relationships between some localities, there are not significant geographic trends; slopes are generally smaller for females than for males (Templeman 1936; Wilder 1953; Conan 1978; Krouse 1981).

MOLT PROBABILITY

For both sexes the probability of molting in any one year declined with increasing size, but more rapidly for females than for males (Fig. 3). Good fits were obtained with exponential regressions (correlations significant, $P < 0.01$) (Fig. 3). In the Bay of Fundy a lobster 60−80 mm L molts about once a year whereas a lobster 140−160 mm L molts on the average every second year, and by extrapolation, a lobster 180−200 mm L probably molts every 3−4 yr. A variety of functions such as linear regressions (Conan and Gundersen 1979), probit analysis (Ennis et al. 1982), and a logistic function (Fogarty et al. 1982) have been used to relate molt frequency to premolt size. The exponential regressions were used in the present study because they provided better fits (high R^2) to the data relating to premolt size and molt probability. Annual molt probability varies with size but remains fairly constant within each size range (Aiken 1980), varying slightly with small annual changes in temperature (Ennis et al. 1982). The probability of molting of the Bay of Fundy lobsters did not decline as rapidly with size increase as reported for lobsters on the outer continental shelf of the United States (Cooper and Uzmann 1977; Fogarty et al. 1982) and for Newfoundland (Ennis et al. 1982). The estimated rapid decline in molt probability may be due to lack of molting data for large lobsters resulting from high exploitation rates and/or trap selectivity for smaller sizes (Ennis et al. 1982; Fogarty et al. 1982).

LONG-TERM GROWTH

Growth increments were highly variable and generally increased with time at liberty but at a higher rate for males than for females (Fig. 4). Increments decreased with increase in size of lobster for similar times at liberty. The largest increments recorded were 57 mm for a 110 mm L premolt male at liberty for 42 mo (four molt periods), and 45 mm for an 80 mm L premolt female at liberty for 36 mo (three molt periods) (Fig. 4). Accurate identification of the number of molts and growth increment per molt of individuals from this type of data is difficult. Yet this long-term, release−recapture growth information is valuable and can be used to estimate growth curves without the necessity of separating out the individual growth increments and molt probabilities or intermolt periods. The following multiple regressions are useful in that all recaptured lobsters showing no growth over a molt

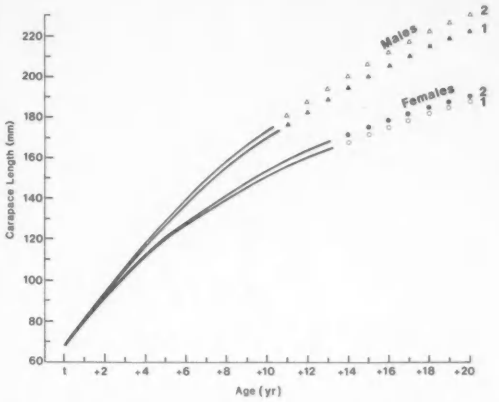

FIG. 5. Growth curves for male and female lobsters estimated from (1) product of annual molt increment and molt probability and (2) multiple regression growth curves. Dotted lines are extrapolated beyond available data.

period can be included as well as those showing large increments over many molt periods. The multiple regressions were highly significant, using the data in Fig. 4.
For males:

$$\Delta L_M = -5.31 + 20.50M + 0.05L_x - 0.09\mu$$

($R^2 = 0.48$; df = 3, 347; $F = 106.8$; $P < 0.01$; SE = 6.77)

For females:

$$\Delta L_M = 4.59 + 14.98M - 0.02L_x - 0.07\mu$$

($R^2 = 0.55$; df = 3, 492; $F = 197.9$; $P < 0.01$; SE = 4.99).

The multiple regression model is not intended to explain the underlying growth processes but to synthesize empirical growth data mimicking growth in length of an average individual lobster.

Use of days or months instead of molt periods (or years) as units of time at liberty did not produce significant ($P > 0.05$) correlations for the multiple regressions. Knowledge of the molt period of lobsters in an area is obviously critical for this multiple regression model.

The term for the number of molt periods in the multiple regression has the largest positive influence on growth increment (beta = 1.6) for both sexes. The interactive term is the next most important factor but is negative (beta = −1.0) for both sexes, modifying the regression by reducing the growth increments with increasing size at release and with the number of molt periods. The term for size at release has the smallest influence on the regression, being negative for females (beta = −0.08) but positive for males (beta = 0.17). This reflects the arithmetic-regressive growth for females and arithmetic-progressive growth for males shown in the premolt−postmolt regressions. The predictive capability of the multiple regression model in this study is limited to the accuracy of available data used, mainly for the two to three molt periods (or years) and in the 60−175 mm premolt L range.

TABLE 2. von Bertalanffy growth parameters for recaptured lobsters tagged in the Bay of Fundy, 1979−80, based on empirical growth curves calculated from (1) product of annual molt increment and probability of molting and (2) multiple regression of premolt L, number of molt periods at liberty, and growth increment. Values in brackets are approximate 95% confidence intervals. Only the available data in size range 67−175 mm L were used to estimate parameters except where otherwise noted.

Sex	Method	k	L_∞	t_0
Male	1	0.065	281	0.76
		(±0.012)	(±28)	(±0.33)
	2	0.068	287	1.19
		(±0.012)	(±27)	(±0.38)
Female	1	0.089	207	0.42
		(±0.005)	(±4)	(±0.24)
	1	0.068[a]	230	0.48
		(±0.004)	(±4)	(±0.38)
	2	0.087	217	0.69
		(±0.002)	(±2)	(±0.10)

[a]Data extrapolated to 68−214 mm L range.

GROWTH CURVES

The growth curves (Fig. 5) derived from (1) the product of the empirical growth curves of annual premolt−postmolt sizes and probability of molting and (2) the multiple regression model were similar for each sex. The von Bertalanffy growth parameters (Table 2) derived from the two sets of empirical growth curves (Fig. 5) were also similar for each sex. This demonstrates that the two empirical models conform well numerically to the von Bertalanffy parameters within the size intervals and data considered. The 95% confidence intervals indicate the k, L_∞, and t_0 overlap for males, but only k and t_0 values overlap for females, using both methods (Table 2). Caution should be used in interpreting t_0 because it is affected by the arbitrary ages assigned to the carapace lengths. The L_∞ for females was estimated at 217 mm L but could be increased to 230 mm L by extrapolating the curves to 214 mm L using method 1. These L_∞ values with confidence intervals are within the size range encountered in the Bay of Fundy (Wolff 1978) and similar to those estimated for lobsters in the Gulf of Maine (Thomas 1973; Cooper and Uzmann 1977; Russell 1980). In the present study, of the 40 412 lobsters measured during 1976−82 on boats fishing for large lobsters in the Bay of Fundy, the largest male caught was 219 mm L and the largest female was 230 mm L; 61 males and 3 females were 200 mm L. The largest ovigerous female encountered was 197 mm L.

General Discussion

The growth parameters estimated in the study are considered accurate for the majority of lobsters encountered in the Bay of Fundy, which are well under 200 mm L. However, additional information, especially for use in the multiple regression model, would be useful for understanding growth

TABLE 3. Molting and egg extrusion of recaptured female lobsters over 1–4 molt periods (yr). Ovigerous females (N = 457) were tagged and released off North Head, Grand Manan, November 15–December 8, 1977. Main molt period considered as August–October of each year.

Period of recapture	Molt period year	Recaptured lobsters		
		N	% molted[a]	% ovigerous
Nov. 1978–June 1979	1	20	75.0	0
Nov. 1979–June 1980	2	12	83.3	100.0
Nov. 1980–June 1981	3	2	100.0	0
Nov. 1981–June 1982	4	3	100.0	100.0

[a]Most nonmolt lobsters had zero increments but one individual with +3- and another with −9-mm increments were considered nonmolters due to measurement variation.

of lobsters larger than 160 mm L and for all lobster sizes at liberty for four or more molt periods. Multiple recapture-release of tagged lobsters would be useful in allowing the growth of individual large lobsters to be followed. Growth of juvenile lobsters 5–60 mm L in the Bay of Fundy is unknown. Despite the lack of knowledge on juvenile growth and assuming lobsters are about 6 yr at 81 mm L (Aiken 1980), the empirical growth curves give a reasonable estimation of the time required for male (about 20 yr) and female lobsters (about 30 yr) to reach 200 mm L from time of hatching in the Bay of Fundy. However, these estimates could vary by ±5 yr but are in general agreement with other field and laboratory studies (Cooper and Uzmann 1977; Mauchline 1977; Aiken 1980).

Clearly, growth of mature male lobsters is more rapid and reaches a higher asymptote than that of mature female lobsters in the Bay of Fundy. This difference in growth rate is caused by reduced growth increment and molting frequency among females compared with males because females allocate energy for egg production as well as growth (Templeman 1933; Aiken and Waddy 1980). Analysis of recapture data from ovigerous females tagged and released in November–December 1977 (Table 3) indicates that one molt period later, 75% had molted, but none was ovigerous, whereas two molt periods later, 83% had molted and 100% were ovigerous again. This assumes lobsters with ≤3-mm increments did not molt. Four molt periods later, all three of the females had molted and were ovigerous again (Table 3). These data confirm that, in general, mature female lobsters in the wild contribute energy to molting and extruding eggs in alternate years. Herrick (1909) also noted that males molted more frequently than females and, on average, females spawned every second year. However, the fact that about 20% of the female lobsters were found to extrude a second batch of eggs without molting (Table 3) supports Aiken and Waddy (1980) in that a few large mature females in the wild may have multiple egg extrusions between molts.

Although the von Bertalanffy growth model for describing growth has been criticized (e.g. Roff 1980) and does not describe the details of discontinuous growth pattern of lobsters, the model nevertheless is suited to the basic stock assessments required for lobster management. The von Bertalanffy model can be integrated with other classical formulations such as the Beverton-Holt yield-per-recruit model (Beverton and Holt 1957) and other production models that have been used on lobsters (e.g. Saila et al. 1979; Fogarty 1980). Some recent yield-per-recruit models for lobsters have circumvented the use of the von Bertalanffy growth parameters and incorporated directly the empirical functions of growth-per-molt and probability of molting (e.g. Caddy 1977). Improved growth models that are to describe discontinuous lobster growth more realistically in the future will have to, for example, incorporate functions that can synchronize size-specific molting and reproductive activity with seasonal changes in temperature.

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Protozoan and Metazoan Parasites of Fishes from the Headwaters of the Parsnip and McGregor Rivers, British Columbia: A Study of Possible Parasite Transfaunations

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ARAI, H. P., AND D. R. MUDRY. 1983. Protozoan and metazoan parasites of fishes from the headwaters of the Parsnip and McGregor rivers, British Columbia: a study of possible parasite transfaunations. Can. J. Fish. Aquat. Sci. 40: 1676–1684.

Results are presented of a study to determine the possible extent of parasite transfaunation across the Continental Divide as a result of a proposed water diversion in northeastern British Columbia. Fish populations in the headwater areas of the McGregor River (Pacific drainage) and of the Parsnip River (Arctic drainage) were sampled during August–November 1976 and during June–September 1977. Eighty-eight species or higher taxonomic groups of parasites were recovered from 1489 host specimens, representing 13 genera and 20 species of fishes. *Eimeria cotti* from *Cottus cognatus* and *Rhabdochona zacconis* from *Catostomus macrocheilus* have not been previously recorded from North America. New Canadian records are *Chloromyxum granulosum*, *C. montschadskii*, *Leptotheca* sp., *Myxidium macrocheili*, *Myxobolus aureatus*, *M. microthecum*, *Neomyxobolus ophiocephalus*, *Unicauda crassicauda*, and *Wardia* sp. Twenty-six parasites show disjunct distributions in the study area. Three forms (*Ceratomyxa shasta*, *Cryptobia salmositica*, and *Haemogregarina irkalukpiki*) are identified as posing the greatest threat to the fisheries resources of the immediate area and also to the downstream areas. Based in part on these studies, the British Columbia Hydro and Power Authority, in a public announcement, suspended engineering studies of the proposed diversion.

ARAI, H. P., AND D. R. MUDRY. 1983. Protozoan and metazoan parasites of fishes from the headwaters of the Parsnip and McGregor rivers, British Columbia: a study of possible parasite transfaunations. Can. J. Fish. Aquat. Sci. 40: 1676–1684.

L'article qui suit contient les résultats d'une étude menée en vue de déterminer le degré possible de transmission parasitaire d'un côté à l'autre de la ligne divisoire continentale à la suite d'un détournement proposé des eaux dans le nord-est de la Colombie-Britannique. Les populations de poissons à la tête des eaux de la rivière McGregor (bassin du Pacifique) et de la rivière Parsnip (bassin de l'Arctique) ont été échantillonnées de août à novembre 1976 inclusivement et de juin à septembre 1977 inclusivement. Quatre-vingt-huit espèces ou groupes taxonomiques plus élevés de parasites ont été récupérés de 1 489 hôtes, représentant 13 genres et 20 espèces de poissons. La présence de *Eimeria cotti* chez *Cottus cognatus* et de *Rhabdocona zacconis* chez *Catostomus macrocheilus* n'avait pas encore été signalée en Amérique du Nord. Les mentions nouvelles pour le Canada sont les suivantes : *Chloromyxum granulosum*, *C. montschadskii*, *Leptotheca* sp., *Myxidium macrocheili*, *Myxobolus aureatus*, *M. microthecum*, *Neomyxobolus ophiocephalus*, *Unicauda crassicauda* et *Wardi* sp. Onze autres espèces de parasites n'avaient pas non plus été signalées au Canada. Dans la région étudiée, 26 parasites montrent des distributions disjointes. Trois formes (*Ceratomyxa shasta*, *Cryptobia salmositica* et *Haemogregarina irkalukpiki*) sont reconnues comme la plus importante menace pour les ressources halieutiques du voisinage immédiat ainsi qu'en aval. Les résultats de cette étude sont en partie responsables de la décision, annoncée publiquement, de la *British Columbia Hydro and Power Authority* de suspendre les études d'ingénierie relatives au projet de détournement.

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THE proposal by the British Columbia Hydro and Power Authority for a diversion of the McGregor River in northeastern British Columbia for hydroelectrical purposes raised a number of concerns regarding the impact of such an undertaking on the environment. This diversion, to be accomplished by the construction of a dam on the midreaches of the river, would create a reservoir that would result in the flow of water into the Parsnip River drainage system. In addition to concerns related to the general effects on the aquatic envi-

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TABLE 1. Fish hosts: numbers and distribution.

	Arctic	Pacific	Total
Catostomus catostomus	51	49	100
C. columbianus	—	3	3
C. commersoni	22	—	22
C. macrocheilus	49	43	92
Coregonus clupeaformis	86	—	86
Cottus asper	—	19	19
C. cognatus	29	23	52
Lota lota	7	9	16
Mylocheilus caurinus	7	22	29
Oncorhynchus nerka	52	18	70
O. tshawytscha	—	57	57
Prosopium coulteri	5	—	5
P. williamsoni	153	145	298
Ptychocheilus oregonensis	33	20	53
Rhinichthys cataractae	20	6	26
Richardsonius balteatus	20	20	40
Salmo gairdneri	100	98	198
Salvelinus malma	101	85	186
S. namaycush	24	13	37
Thymallus arcticus	100	—	100
Total	859	630	1489

ronment, the possibility of faunal exchanges across the Continental Divide was also considered. It was recognized by B.C. Hydro that fish parasites of economic and pathogenic significance could also be involved in the two-way transfer of fauna.

Hoffman (1970) offers documentation that at least 40 animal parasites of freshwater fishes (5 protozoans, 31 monogeneans, 5 digeneans, 3 nematodes, 3 acanthocephalans, and 3 copepods) have become established on other continents through the transfer of infected fishes. In spite of this information, very few diversion projects in North America have included the examination of this potential for parasite transfaunation. The Garrison Diversion Project study (Anonymous 1976) included a literature review that was basically restricted to a recompilation of information provided by Hoffman (1967) and with very little site-specific data. However, the Biology Committee involved in the impact assessment indicated that interbasin transfer of some pathogens was likely. In another study, Arthur et al. (1976), through field and laboratory investigations, examined the possibility of transfaunation of fish parasites between the Alsek and Yukon river systems in the Yukon Territory. Disjunct distributions of a large number of parasites were encountered in the headwater regions of these rivers. They concluded that significant harmful effects might arise if transfers were to occur as a result of the water diversion.

The present study reports on the prevalence and intensity of infection of protozoan and metazoan parasites recovered from a large number of fishes collected from the headwaters of the Parsnip and McGregor rivers and discusses implications of potential transfaunation of parasites.

Materials and Methods

STUDY AREA

The lake and stream systems studied are located approximately 70 km northeast of Prince George, British Columbia. The McGregor River originates in the Rocky Mountains near the Alberta border and flows northwesterly for about 100 km to the junction with its major tributary, Herrick Creek. At Herrick Creek, the McGregor River turns south and flows to the southwest for 15 km, passing through the McGregor Range at Lower Canyon (proposed damsite). It is joined by Otter Creek, which drains Otter Lake, and then continues for about 35 km to its confluence with the Fraser River, about 55 km northeast of Prince George.

James Creek, one of the tributaries of Herrick Creek, has its headwaters in a low divide (Arctic Divide) containing three lakes. Two of these lakes, Portage Lake and Pacific Lake, drain southeasterly into James Creek. The third, Arctic Lake, drains northwesterly into a small unnamed creek flowing into the Parsnip River, a tributary of the Peace River.

The Parsnip River flows southwesterly for about 24 km until it meets the drainage from Arctic Lake in a wide swampy plain in the Rocky Mountain Trench. It then follows the trench in a northwesterly direction for about 130 km to reach Williston Lake reservoir. Between its origin and Williston Lake, the Parsnip River is joined by Missinka River, Wichcika Creek, Hominka River, Table River, Woododilinka Creek, Anzac River, Reynolds Creek, and Misinchinka River.

Host fishes were collected using gill nets and electrofishers and by angling. These collections were made during August–November 1976 and June–September 1977. A total of 859 fishes of 17 species from the Parsnip River (Arctic drainage) and 630 specimens of 16 species from the McGregor River (Pacific drainage) were examined for protozoan and metazoan parasites (Table 1). *Oncorhynchus nerka* that were collected were the lacustrine stock of sockeye salmon, the kokanee, and not the anadromous form. *Oncorhynchus tshawytscha* included eight spawning chinooks and the remainder were of the 0+ and 1+ year classes.

HOST EXAMINATIONS

Fish specimens were tagged, frozen, and delivered to the laboratory for examination. Host weight, fork length, and sex were recorded. The tissues and organs examined and dissected for parasites included skin, fins, eyes, nasal cavities, body musculature, buccal cavity, gills, esophagus, heart, stomach, pyloric caeca, intestine, mesenteries, gall bladder, liver, swim bladder, kidneys, ureters, coelom, and gonads.

Semipermanent slides of tissue samples from gills, gall bladder, pyloric caeca, and kidneys were prepared for each host and later examined for protozoan parasites. Whole fish heads or parts of the skull were fixed in 10% formalin and later examined for *Myxosoma cerebralis* following the procedure of Gillespie et al. (1974). Thin blood smears were prepared in the field, fixed with absolute methanol, and stained with Giemsa's stain. Slides of blood and tissue smears were examined for protozoans using a Leitz Ortholux phase-contrast microscope at magnifications up to 400×.

The metazoan parasites were fixed in a mixture of ethanol–acetic acid–formalin. The nematodes were transferred to glycerine–ethanol for clearing and examined as temporary whole mounts. Representative specimens of other helminths

were stained in Grenacher's borax carmine or acetocarmine and mounted in Canada balsam. Dissected appendages of copepods were studied in a glycerine jelly preparation.

Whenever appropriate, exact counts of metazoan parasites present were made to determine the intensity of infection (mean number of parasites of a given species per infected host). Prevalence, the number of infected hosts per total number of hosts examined, was recorded for each parasite species. These values are provided in the account of each of the species. Nomenclature of parasites and of the fish hosts follow that of Margolis and Arthur (1979) and Scott and Crossman (1973), respectively.

Results

Eighty-eight species or higher taxonomic groupings of parasites were recovered from the 1489 host specimens representing 13 genera and 20 species of fishes. Included among these parasites were 24 protozoans, 10 monogeneans, 11 trematodes, 15 cestodes, 18 nematodes, 5 acanthocephalans, and 5 copepods. For each of the parasite species recorded, the following information is given: stage of maturity of the parasite (if other than adult), site(s) in or on the host, host name, prevalence and intensity of infection (where appropriate) for hosts collected in the Pacific drainage (P) and Arctic drainage (A), and appropriate comments. An asterisk preceding a host name indicates a new host record.

PROTOZOA

Eimeria cotti Gauthier, 1921; pyloric caeca: **Cottus cognatus* (A = 8/29; P = 2/23); not previously reported from North America

Eimeria sp.; pyloric caeca; *Oncorhynchus nerka* (A = 0/52; P = 1/18), *Salmo gairdneri* (A = 1/100; P = 1/98), *Salvelinus malma* (A = 9/101; P = 4/85), *Thymallus arcticus* (A = 2/100; P = 0/0)

Haemogregarina irkalukpiki Laird, 1961; blood (erythrocytes); **Salvelinus malma* (A = 0/101; P = 2/85); not previously reported from British Columbia

Dactylosoma salvelini Fantham, Porter and Richardson, 1942; blood; **Salvelinus malma* (A = 0/101; P = 2/85); previously known only from a single report from Quebec (Fantham et al. 1942); stages resembling merozoites were observed on two blood smears

Nosema sp.; pyloric caeca, intestine; **Prosopium williamsoni* (A = 4/153; P = 2/145), **Thymallus arcticus* (A = 3/100; P = 0/0)

Pleistophora sp.; pyloric caeca, intestine; **Richardsonius balteatus* (A = 0/20; P = 1/20), **Salmo gairdneri* (A = 0/100; P = 4/98)

Ceratomyxa shasta Noble, 1950; gall bladder, pyloric caeca, intestine; **Oncorhynchus tshawytscha* (A = 0/0; P = 4/57); identification based on spore morphology

Ceratomyxa sp.; intestine; **Catostomus macrocheilus* (A = 0/49; P = 1/43)

Chloromyxum granulosum Davis, 1917; gall bladder; **Catostomus macrocheilus* (A = 0/49; P = 1/43); not previously reported from Canada; spores observed agree with the description provided by Kudo (1920) in having converging valvular ridges

Chloromyxum montschadskii Shul'man, 1962; gall bladder; **Ptychocheilus oregonensis* (A = 1/33; P = 0/20); not previously reported from Canada; spores observed have polar capsules of unequal size as described by Shul'man (1966) for *C. montschadskii* but differ in having ridges

Henneguya zschokkei (Gurley, 1893) Doflein, 1901; body musculature, gills, kidneys; **Cottus cognatus* (A = 0/29; P = 3/23), **Prosopium williamsoni* (A = 10/153; P = 19/145), **Rhinichthys cataractae* (A = 1/20; P = 0/6), **Richardsonius balteatus* (A = 1/20; P = 0/20), **Thymallus arcticus* (A = 4/100; P = 0/0)

Leptotheca sp.; kidneys; **Salmo gairdneri* (A = 5/100; P = 6/98); not previously reported from Canada

Myxidium macrocheili Mitchell, 1967; gall bladder, intestine; **Catostomus macrocheilus* (A = 14/49; P = 12/43); not previously reported from Canada

Myxidium spp.; kidney; **Oncorhynchus tshawytscha* (A = 0/0; P = 1/57), **Prosopium williamsoni* (A = 1/153; P = 0/145)

Myxobolus aureatus Ward, 1919; gills; **Lota lota* (A = 0/7; P = 1/9), **Mylocheilus caurinus* (A = 1/7; P = 5/22), **Ptychocheilus oregonensis* (A = 0/33; P = 1/20), **Richardsonius balteatus* (A = 2/20; P = 1/20); not previously reported from Canada

Myxobolus microthecum (Meglitsch, 1942); gall bladder, kidney, intestine; **Rhinichthys cataractae* (A = 7/20; P = 3/6), **Richardsonius balteatus* (A = 2/20; P = 0/20); not previously reported from Canada

Myxobolus spp.; gall bladder, intestine, heart, kidney, liver; *Catostomus catostomus* (A = 30/51; P = 45/49), *C. columbianus* (A = 0/0; P = 1/3), *C. commersoni* (A = 11/22; P = 0/0), *C. macrocheilus* (A = 15/49; P = 21/43), *Coregonus clupeaformis* (A = 3/86; P = 0/0), *Cottus cognatus* (A = 1/29; P = 7/23), *Lota lota* (A = 4/7; P = 2/9), *Mylocheilus caurinus* (A = 6/7; P = 20/22), *Oncorhynchus nerka* (A = 2/52; P = 0/18), *O. tshawytscha* (A = 0/0; P = 1/57), *Ptychocheilus oregonensis* (A = 32/33; P = 20/20), *Rhinichthys cataractae* (A = 6/20; P = 1/6), *Richardsonius balteatus* (A = 10/20; P = 12/20), *Salvelinus malma* (A = 5/101; P = 0/85), *Thymallus arcticus* (A = 1/100; P = 0/0)

Neomyxobolus ophiocephalus Chen, 1960; kidney; **Catostomus catostomus* (A = 0/51; P = 6/49), *C. commersoni* (A = 1/22; P = 0/0), **C. macrocheilus* (A = 8/49; P = 2/43); not previously reported from Canada

Unicauda crassicauda Kudo, 1934; gills, gall bladder, intestine, kidney; **Ptychocheilus oregonensis* (A = 20/33; P = 18/20); not previously reported from Canada; although our spores are somewhat larger (10.5 × 17.0 μm), they conform with those in the description of *U. crassicauda* reported from *Campostoma anomalum* from Illinois by Meglitsch (1937)

Wardia sp.; kidney; **Cottus cognatus* (A = 1/29; P = 1/23), **Lota lota* (A = 2/7; P = 1/9), **Richardsonius balteatus* (A = 2/20; P = 0/20); not previously reported from Canada

Epistylis sp.; gills; *Cottus asper* (A = 0/0; P = 3/19), *Oncorhynchus nerka* (A = 1/52; P = 0/18)

Trichodina sp.; gills; *Catostomus catostomus* (A = 4/51; P =

0/49), *Salmo gairdneri* (A = 3/100; P = 0/98)

Cryptobia salmositica Katz, 1951; blood; *Oncorhynchus tshawytscha* (adults); (A = 0/0; P = 1/4)

Dermocystidium sp.; gills; *Coregonus clupeaformis* (A = 1/86; P = 0/0), *Lota lota* (A = 0/7; P = 1/9), *Prosopium williamsoni* (A = 3/153; P = 1/145), *Thymallus arcticus* (A = 2/100; P = 0/0); the taxonomic position of *Dermocystidium* is uncertain (Hoffman 1967); a species of *Dermocystidium* was identified as the primary cause of a massive fish kill in the Nipkish River, Vancouver Island (Hoskins et al. 1976)

MONOGENEA

Acolpenteron catostomi Foschthal and Allison, 1942; ureters; *Catostomus catostomus* (A = 3/51, 4.0; P = 2/49, 17.0), **C. macrocheilus* (A = 2/49, 5.0; P = 1/43, 10.0); not previously reported from British Columbia

Anoncohaptor anomalum Mueller, 1938; gills; *Catostomus catostomus* (A = 1/51, 3.0; P = 1/49, 2.0); *C. commersoni* (A = 3/22, 1.0; P = 0/0, 0.0), **C. macrocheilus* (A = 2/49, 1.0; P = 0/43, 0.0); not previously reported from British Columbia

Gyrodactyloidea gen. spp.; gills; *Mylocheilus caurinus* (A = 1/7, 3.0; P = 0/22, 0.0), *Prosopium williamsoni* (A = 4/153, 1.5; P = 2/145, 2.0), *Ptychocheilus oregonensis* (A = 1/33, 1.0; P = 0/20, 0.0)

Pellucidhaptor pellucidhaptor Price and Mizelle, 1964; gills; **Richardsonius balteatus* (A = 2/20, 4.0; P = 0/20, 0.0)

Pseudomurraytrema copulata (Mueller, 1938) Bykhovsky, 1957; gills; **Catostomus catostomus* (A = 5/51, 7.6; P = 3/49, 3.6), *C. commersoni* (A = 8/22, 6.5; P = 0/0, 0.0), **C. macrocheilus* (A = 28/49, 12.8; P = 11/43, 15.1); not previously reported from British Columbia

Tetraonchus alaskensis Price, 1937; gills; **Salvelinus malma* (A = 0/101, 0.0; P = 5/85, 2.8); not previously reported from British Columbia

Tetraonchus borealis (Olsson, 1893) Monticelli, 1905; gills; *Thymallus arcticus* (A = 34/100, 6.1; P = 0/0, 0.0); not previously reported from British Columbia

Tetraonchus variabilis Mizelle and Webb, 1953; gills; **Prosopium williamsoni* (A = 30/153, 2.9; P = 30/145, 3.9)

Octomacrum lanceatus Mueller, 1934; gills; *Catostomus macrocheilus* (A = 1/49, 1.0; P = 0/43, 0.0), **Oncorhynchus tshawytscha* (A = 0/0, 0.0; P = 1/57, 1.0)

Octomacrum microfibulum Hargis, 1952; gills; **Mylocheilus caurinus* (A = 0/7, 0.0; P = 1/22, 1.0)

TREMATODA

Allocreadium isoporum (Looss, 1894) Odhner, 1901; intestine; **Mylocheilus caurinus* (A = 1/7, 2.0; P = 6/22, 27.5), **Ptychocheilus oregonensis* (A = 1/33, 2.0; P = 0/20, 0.0); not previously reported from British Columbia

Bunodera luciopercae (O. F. Mueller, 1776) Luhe, 1909; intestine; *Salmo gairdneri* (A = 8/100, 18.6; P = 3/98, 85.6)

Crepidostomum farionis (O. F. Mueller, 1780) Luhe, 1909; intestine; **Coregonus clupeaformis* (A = 3/86, 3.0; P = 0/0, 0.0), **Cottus cognatus* (A = 1/29, 4.0; P = 0/23, 0.0), *Lota lota* (A = 1/7, 1.0; P = 2/9, 1.0), *Oncorhynchus nerka* (A = 3/52, 1.3; P = 1/18, 1.0), **O. tshawytscha* (A = 0/0, 0.0; P = 1/57, 2.0), *Prosopium williamsoni* (A = 3/153, 11.3; P = 8/145, 3.5), *Salmo gairdneri* (A = 28/100, 22.8; P = 24/98, 39.3), *Salvelinus malma* (A = 15/101, 2.1; P = 22/85, 12.7), *Thymallus arcticus* (A = 14/100, 3.9; P = 0/0, 0.0)

Phyllodistomum sp.; ureters; **Oncorhynchus nerka* (A = 7/52, 1.0; P = 0/18, 0.0), **Salmo gairdneri* (A = 4/100, 10.0; P = 1/98, 4.0), **Salvelinus namaycush* (A = 0/0, 0.0; P = 1/13, 1.0)

Brachyphallus crenatus (Rudolphi, 1802) Odhner, 1905; intestine; **Oncorhynchus tshawytscha* (A = 0/0, 0.0; P = 2/57, 3.0)

Genolinea oncorhynchi Margolis and Adams, 1962; intestine; **Oncorhynchus tshawytscha* (A = 0/0, 0.0; P = 1/57, 1.0)

Lampritrema miescheri (Zschokke, 1890) Margolis, 1962; intestine; **Oncorhynchus tschawytscha* (A = 0/0, 0.0; P = 1/57, 1.0)

Diplostomum sp. 1 (metacercaria); brain; *Coregonus clupeaformis* (A = 1/86, 1.0; P = 0/0, 0.0), *Mylocheilus caurinus* (A = 3/7, 30.3; P = 16/22, 17.5), *Prosopium williamsoni* (A = 0/153, 0.0; P = 1/145, 2.0), *Ptychocheilus oregonensis* (A = 1/33, 27.0; P = 0/20, 0.0), *Richardsonius balteatus* (A = 2/20, 6.5; P = 0/20, 0.0), *Salmo gairdneri* (A = 0/100, 0.0; P = 3/98, 3.0)

Diplostomum sp. 2 (metacercaria); vitreous humor; *Catostomus catostomus* (A = 0/51, 0.0; P = 1/49, 1.0), *C. macrocheilus* (A = 1/49, 1.0; P = 1/43, 3.0), *Coregonus clupeaformis* (A = 5/86, 17.5; P = 0/0, 0.0), *Cottus cognatus* (A = 1/29, 73.0; P = 1/23, 7.0), *Lota lota* (A = 1/7, 24.0; P = 0/9, 0.0), *Oncorhynchus nerka* (A = 7/52, 1.8; P = 0/18, 0.0), *Prosopium williamsoni* (A = 3/153, 11.6; P = 5/145, 8.8), *Ptychocheilus oregonensis* (A = 2/33, 1.5; P = 0/20, 0.0), *Richardsonius balteatus* (A = 2/20, 4.0; P = 2/20, 7.0), *Salmo gairdneri* (A = 4/100, 32.0; P = 1/98, 2.0), *Salvelinus malma* (A = 8/101, 11.8; P = 2/85, 10.5), *S. namaycush* (A = 11/24, 95.2; P = 5/13, 21.4); this form resembles *D. destructor* Szidat and Nani, 1971, from South America

Neascus sp. (metacercaria); skin; *Catostomus catostomus* (A = 0/51, 0.0; P = 3/49, 8.6), **Oncorhynchus tshawytscha* (A = 0/0, 0.0; P = 1/57, 2.0), *Ptychocheilus oregonensis* (A = 1/33, 171.0; P = 0/20, 0.0)

Tetracotyle sp. (metacercaria); pericardium, visceral mesenteries; *Catostomus catostomus* (A = 1/51, 6.0; P = 3/49, 8.6), *C. commersoni* (A = 4/22, 26.3; P = 0/0, 0.0), *C. macrocheilus* (A = 2/49, 89.5; P = 3/43, 93.6), *Coregonus clupeaformis* (A = 5/86, 8.8; P = 0/0, 0.0), *Cottus cognatus* (A = 1/29, 4.0; P = 2/23, 16.0), *Mylocheilus caurinus* (A = 0/7, 0.0; P = 3/22, 2.6), *Oncorhynchus nerka* (A = 1/52, 4.0; P = 1/18, 1.0), *Prosopium williamsoni* (A = 2/153, 21.0; P = 7/145, 15.7), *Ptychocheilus oregonensis* (A = 12/33,

10.8; P = 7/20, 155.2), *Rhinichthys cataractae* (A = 1/20, 15.0; P = 0/6, 0.0), *Richardsonius balteatus* (A = 4/20, 9.5; P = 5/20, 105.0), *Salmo gairdneri* (A = 1/100, 1.0; P = 6/98, 11.6), *Salvelinus malma* (A = 1/101, 5.0; P = 4/85, 4.0), *S. namaycush* (A = 3/24, 7.3; P = 1/13, 55.0), *Thymallus arcticus* (A = 1/100, 8.0; P = 0/0, 0.0)

CESTOIDEA

Caryophyllidae gen. sp.; intestine; *Catostomus catostomus* (A = 5/51, 1.4; P = 5/49, 2.0), *C. macrocheilus* (A = 4/49, 1.2; P = 3/43, 2.3)

Glaridacris catostomi Cooper, 1920; intestine; *Catostomus catostomus* (A = 5/51, 2.1; P = 12/49, 2.1), *C. commersoni* (A = 1/22, 1.0; P = 0/0, 0.0)

Glaridacris sp.; intestine; *Catostomus macrocheilus* (A = 1/49, 1.0; P = 0/43, 0.0)

Glaridacris vogei Mackiewicz, 1976; intestine; *Catostomus macrocheilus* (A = 2/49, 13.0; P = 0/43, 0.0)

Hunterella nodulosa Mackiewicz and McCrae, 1962; intestine; *Catostomus commersoni* (A = 7/22, 8.8; P = 0/0, 0.0), *C. macrocheilus* (A = 1/49, 2.0; P = 0/43, 0.0); although reported by Threlfall and Hanek (1970) from *C. catostomus*, this parasite is probably restricted to *C. commersoni* and the closely related species, *C. macrocheilus* and *C. ardens*

Monobothrium sp.; intestine; *Catostomus catostomus* (A = 1/51, 1.0; P = 0/49, 0.0), *C. commersoni* (A = 1/22, 9.0; P = 0/0, 0.0)

Proteocephalus ptychocheilus Faust, 1920; intestine; *Ptychocheilus oregonensis* (A = 20/33, 6.3; P = 10/20, 3.5)

Proteocephalus salmonidicola Alexander, 1951; intestine; *Salvelinus malma* (A = 6/101, 25.8; P = 11/85, 32.4)

Proteocephalus sp.; intestine, pyloric caeca; *Coregonus clupeaformis* (A = 2/86, 39.0; P = 0/0, 0.0), *Cottus asper* (A = 0/0, 0.0; P = 2/19, 30.0), *Mylocheilus caurinus* (A = 0/7, 0.0; P = 3/22, 1.0), *Oncorhynchus nerka* (A = 3/52, 33.6; P = 1/18, 2.0), *Prosopium williamsoni* (A = 8/153, 7.4; P = 3/145, 5.6), *Salvelinus malma* (A = 4/101, 1.2; P = 2/85, 1.0)

Proteocephalus tumidocollus Wagner, 1953; intestine; **Salmo gairdneri* (A = 17/100, 17.1; P = 10/98, 5.5); not previously reported from British Columbia

Bothriocephalus opsariichthydis Yamaguti, 1934; intestine; *Mylocheilus caurinus* (A = 1/7, 1.0; P = 0/22, 0.0), **Ptychocheilus oregonensis* (A = 16/33, 8.4; P = 7/20, 3.0); not previously reported in Canada; widely distributed in Asia and eastern Europe and recently introduced into the United States (Hoffman 1980)

Diphyllobothrium spp. (plerocercoid); visceral mesenteries, liver; *Coregonus clupeaformis* (A = 10/86, 6.7; P = 0/0, 0.0), *Oncorhynchus nerka* (A = 37/52, 2.2; P = 4/18, 1.0), *Prosopium williamsoni* (A = 5/153, 4.4; P = 7/145, 4.7), *Salmo gairdneri* (A = 1/100, 1.0; P = 2/98, 2.0), *Salvelinus malma* (A = 1/101, 1.0; P = 0/85, 0.0), *S. namaycush* (A = 2/24, 1.3; P = 2/13, 2.5), *Thymallus arcticus* (A = 2/100, 2.0; P = 0/0, 0.0)

Eubothrium salvelini (Schrank, 1790) Nybelin, 1922; pyloric caeca; *Oncorhynchus nerka* (A = 4/52, 3.7; P = 0/18, 0.0), **O. tshawytscha* (A = 0/0, 0.0; P = 6/57, 1.8), **Prosopium williamsoni* (A = 1/153, 1.0; P = 3/145, 4.6), *Salmo gairdneri* (A = 3/100, 4.3; P = 1/98, 1.0), *Salvelinus malma* (A = 40/101, 18.1; P = 38/85, 14.7), *S. namaycush* (A = 9/24, 9.6; P = 13/13, 27.3)

Ligula intestinalis (Linnaeus, 1758) (plerocercoid); coelom; **Cottus cognatus* (A = 1/29, 1.0; P = 0/23, 0.0), *Mylocheilus caurinus* (A = 0/7, 0.0; P = 1/22, 1.0), *Richardsonius balteatus* (A = 3/20, 2.6; P = 0/20, 0.0)

Phyllobothrium sp.; intestine; *Oncorhynchus tshawytscha* (A = 0/0, 0.0; P = 2/57, 2.5); adults of members of this genus are parasites of elasmobranch fishes

NEMATHELMINTHES

Hysterothylacium brachyurum (Ward and Magath, 1917) Deardorff and Overstreet, 1981; pyloric caeca, intestine; *Lota lota* (A = 1/7, 2.0; P = 4/9, 2.2), *Salvelinus malma* (A = 2/101, 1.0; P = 0/85, 0.0)

Raphidascaris acus (Bloch, 1779) Railliet and Henry, 1915; intestine; **Ptychocheilus oregonensis* (A = 2/33, 2.0; P = 0/20, 0.0); not previously reported from British Columbia

Eustrongylides sp. (larva); coelom, stomach wall, swim bladder, body musculature, liver; **Cottus cognatus* (A = 1/29, 1.0; P = 0/23, 0.0), **Lota lota* (A = 0/7, 0.0; P = 2/9, 4.0), *Mylocheilus caurinus* (A = 1/7, 1.0; P = 0/22, 0.0), *Prosopium williamsoni* (A = 6/153, 2.0; P = 5/145, 1.6), **Ptychocheilus oregonensis* (A = 0/33, 0.0; P = 2/20, 1.0), *Salmo gairdneri* (A = 0/100, 0.0; P = 1/98, 2.0), *Salvelinus malma* (A = 3/101, 1.3; P = 3/85, 1.6)

Philometroides huronensis Uhazy, 1976; fins; **Catostomus catostomus* (A = 1/51, 3.0; P = 5/49, 2.8), *C. commersoni* (A = 1/21, 4.0; P = 0/0, 0.0), **C. macrocheilus* (A = 6/49, 1.1; P = 0/43, 0.0); not previously reported from British Columbia

Philonema agubernaculum Simon and Simon, 1936; coelom; **Prosopium williamsoni* (A = 4/153, 6.0; P = 2/145, 2.0), *Salmo gairdneri* (A = 3/100, 17.0; P = 1/98, 3.0)

Philonema oncorhynchi Kuitunen-Ekbaum, 1933; coelom; **Oncorhynchus tshawytscha* (A = 0/0, 0.0; P = 1/57, 1.0)

Philonema sp.; coelom; *Coregonus clupeaformis* (A = 1/86, 1.0; P = 0/0, 0.0), *Oncorhynchus nerka* (A = 1/52, 1.0; P = 1/18, 7.0), *Prosopium williamsoni* (A = 2/153, 1.5; P = 6/145, 2.1), *Salmo gairdneri* (A = 3/100, 13.6; P = 7/98, 1.8), *Salvelinus malma* (A = 4/101, 9.5; P = 1/85, 2.0), **Thymallus arcticus* (A = 1/100, 1.0; P = 0/0, 0.0)

Haplonema hamatulum Moulton, 1931; intestine; *Lota lota* (A = 4/7, 7.7; P = 2/9, 8.0), **Prosopium williamsoni* (A = 0/153, 0.0; P = 3/145, 2.0), **Salmo gairdneri* (A = 0/100, 0.0; P = 3/98, 2.0), **Salvelinus malma* (A = 2/101, 4.5; P = 0/85, 0.0); not previously reported from British Columbia

Truttaedacnitis truttae (Fabricius, 1794) Petter, 1974; pyloric caeca; *Prosopium williamsoni* (A = 15/153, 5.6; P = 0/145, 0.0), *Salmo gairdneri* (A = 3/100, 3.0;

P = 0/98, 0.0), *Salvelinus malma* (A = 6/101, 3.8; P = 0/85, 0.0), *S. namaycush* (A = 2/24, 3.5; P = 0/13, 0.0)

Cystidicola farionis Fisher, 1798; swim bladder; *Prosopium williamsoni* (A = 9/153, 8.1; P = 0/145, 0.0), **Salvelinus malma* (A = 6/101, 3.8; P = 1/85, 1.0), *S. namaycush* (A = 3/24, 7.0; P = 0/13, 0.0)

Cystidicoloides tenuissima (Zeder, 1800) Rasheed, 1965; stomach; *Salmo gairdneri* (A = 5/100, 21.2; P = 6/98, 36.0), *Salvelinus malma* (A = 0/101, 0.0; P = 4/98, 10.2), **Thymallus arcticus* (A = 1/100, 19.0; P = 0/0, 0.0)

Rhabdochona canadensis Moravec and Arai, 1971; intestine; **Salvelinus malma* (A = 1/101, 2.0; P = 1/85, 3.0); not previously reported from British Columbia

Rhabdochona cascadilla Wigdor, 1918; intestine; *Mylocheilus caurinus* (A = 0/7, 0.0; P = 2/22, 3.5), *Ptychocheilus oregonensis* (A = 1/33, 1.0; P = 0/20, 0.0), *Richardsonius balteatus* (A = 1/20, 1.0; P = 1/20, 3.0)

Rhabdochona cotti Gustafson, 1949; intestine; *Cottus cognatus* (A = 3/29, 2.0; P = 6/23, 1.6)

Rhabdochona kisutchi Margolis, Moravec and McDonald, 1975; intestine; **Oncorhynchus nerka* (A = 0/52, 0.0; P = 1/18, 1.0), **Prosopium williamsoni* (A = 0/153, 0.0; P = 1/145, 3.0), **Salmo gairdneri* (A = 0/100, 0.0; P = 14/98, 51.6), **Salvelinus malma* (A = 6/101, 8.5; P = 16/85, 25.9)

Rhabdochona milleri Choquette, 1951; intestine; **Prosopium williamsoni* (A = 0/153, 0.0; P = 4/145, 11.0), **Rhinichthys cataractae* (A = 3/20, 1.6; P = 0/6, 0.0)

Rhabdochona zacconis Yamaguti, 1935; intestine; **Catostomus macrocheilus* (A = 8/49, 5.1; P = 4/43, 1.2); not previously reported from North America

Rhabdochona spp.; intestine; *Catostomus catostomus* (A = 5/51, 1.2; P = 0/49, 0.0), *C. macrocheilus* (A = 4/49, 3.0; P = 1/43, 1.0), *Cottus cognatus* (A = 1/29, 2.0; P = 3/23, 2.6), *Mylocheilus caurinus* (A = 0/7, 0.0; P = 3/22, 4.0), *Oncorhynchus tshawytscha* (A = 0/0, 0.0; P = 1/57, 1.0), *Prosopium williamsoni* (A = 3/153, 1.0; P = 10/145, 6.0), *Ptychocheilus oregonensis* (A = 2/33, 4.5; P = 0/20, 0.0), *Richardsonius balteatus* (A = 2/20, 1.0; P = 0/20, 0.0), *Salmo gairdneri* (A = 17/100, 17.1; P = 9/98, 21.7), *Salvelinus malma* (A = 4/101, 3.0; P = 9/85, 35.2)

ACANTHOCEPHALA

Neoechinorhynchus cristatus Lynch, 1936; intestine; *Catostomus catostomus* (A = 8/51, 12.6; P = 7/49, 4.0), *C. commersoni* (A = 4/22, 4.5; P = 0/0, 0.0), *C. macrocheilus* (A = 33/49, 10.1; P = 9/43, 13.0)

Neoechinorhynchus cylindratus (Van Cleave, 1913) Van Cleave, 1919; intestine; **Richardsonius balteatus* (A = 9/20, 4.6; P = 0/20, 0.0); not previously reported from British Columbia

Neoechinorhynchus rutili (O. F. Mueller, 1780) Hamann, 1892; intestine; **Coregonus clupeaformis* (A = 3/86, 3.0; P = 0/0, 0.0), *Lota lota* (A = 1/7, 9.0; P = 0/9, 0.0), *Oncorhynchus nerka* (A = 47/52, 4.4; P = 1/18, 3.0), **Prosopium coulteri* (A = 1/5, 1.0; P = 0/0, 0.0), *P. williamsoni* (A = 10/153, 1.7; P = 5/145, 2.0), *Richardsonius balteatus* (A = 3/20, 2.6; P = 0/20, 0.0), *Salmo gairdneri* (A = 21/100, 5.9; P = 2/98, 16.5), *Salvelinus malma* (A = 48/101, 3.6; P = 8/85, 3.5), *S. namaycush* (A = 12/24, 13.8; P = 3/13, 20.6), *Thymallus arcticus* (A = 13/100, 2.4; P = 0/0, 0.0)

Octospinifer macilentus Van Cleave, 1919; intestine; *Catostomus catostomus* (A = 2/51, 3.0; P = 0/49, 0.0), *C. commersoni* (A = 1/22, 2.0; P = 0/0, 0.0), **C. macrocheilus* (A = 5/49, 3.6; P = 7/43, 3.7); not previously reported from British Columbia

Pomphorhynchus bulbocolli (Linkins, 1919); intestine; *Catostomus commersoni* (A = 6/22, 103.0; P = 0/0, 0.0), **C. macrocheilus* (A = 9/49, 8.8; P = 0/43, 0.0), **Coregonus clupeaformis* (A = 1/86, 1.0; P = 0/0, 0.0), *Prosopium williamsoni* (A = 1/153, 15.0; P = 0/145, 0.0), *Ptychocheilus oregonensis* (A = 1/33, 3.0; P = 0/20, 0.0), *Salmo gairdneri* (A = 1/100, 1.0; P = 0/98, 0.0)

COPEPODA

Ergasilus nerkae Roberts, 1963; gills; **Catostomus commersoni* (A = 1/22, 5.0; P = 0/0, 0.0), *C. macrocheilus* (A = 9/49, 8.8; P = 0/43, 0.0), **Coregonus clupeaformis* (A = 10/86, 8.6; P = 0/0, 0.0), *Mylocheilus caurinus* (A = 1/7, 1.0; P = 3/22, 1.3), *Oncorhynchus nerka* (A = 0/52, 0.0; P = 7/18, 8.8), *Ptychocheilus oregonensis* (A = 5/33, 3.2; P = 0/20, 0.0), *Salmo gairdneri* (A = 1/100, 7.0; P = 0/98, 0.0), **Thymallus arcticus* (A = 1/100, 2.0; P = 0/0, 0.0)

Salmincola californiensis (Dana, 1853) Wilson, 1915; gills, fins; **Oncorhynchus tshawytscha* (A = 0/0, 0.0; P = 1/57, 1.0), *Salmo gairdneri* (A = 12/100, 1.1; P = 11/98, 2.5), **Salvelinus namaycush* (A = 9/24, 5.2; P = 0/13, 0.0)

Salmincola edwardsii (Olsson, 1869) Wilson, 1915; gills, fins; **Prosopium williamsoni* (A = 0/153, 0.0; P = 1/145, 1.0), *Salvelinus malma* (A = 3/101, 6.6; P = 26/85, 3.1), *S. namaycush* (A = 9/24, 5.2; P = 7/13, 1.8)

Salmincola extensus (Kessler, 1868) Kabata, 1969; fins; *Prosopium williamsoni* (A = 0/153, 0.0; P = 2/145, 1.0)

Salmincola thymalli (Kessler, 1868) Wilson, 1915; gills; **Prosopium williamsoni* (A = 15/153, 1.7; P = 14/145, 1.5), *Thymallus arcticus* (A = 45/100, 2.4; P = 0/0, 0.0)

Discussion

Results of this study include two parasite species not previously recorded from North America: *Eimeria cotti* from *Cottus cognatus* and *Rhabdochona zacconis* from *Catostomus macrocheilus*. Nine other parasite species have not been previously reported from Canada.

Comparison of the parasite faunas found in hosts from the Pacific and Arctic drainages within the study area indicates that 26 taxa have a disjunct distribution (Table 2). Of these, 17 were recovered from hosts that occur in both

TABLE 2. Parasites with disjunct distributions in the study area.

	Life cycle (direct or indirect)	Host distribution (Arctic/Pacific)
Pacific only		
Ceratomyxa shasta	Direct	P
Ceratomyxa sp.	Direct	A/P
Chloromyxum granulosum	Direct	A/P
Cryptobia salmositica	Indirect	P
Dactylosoma salvelini	Indirect	A/P
Haemogregarina irkalukpiki	Indirect	A/P
Pleistophora sp.	Direct	A/P
Tetraonchus alaskensis	Direct	A/P
Octomacrum microfibulum	Direct	A/P
Brachyphallus crenatus	Indirect	P
Genolinea oncorhynchi	Indirect	P
Lampritrema miescheri	Indirect	P
Philonema oncorhynchi	Indirect	P
Salmincola extensus	Direct	A/P
Arctic only		
Chloromyxum montschadskii	Direct	A/P
Trichodina sp.	Direct	A/P
Pellucidhaptor pellucidhaptor	Direct	A/P
Tetraonchus borealis	Direct	A
Glaridacris sp.	Indirect	A/P
Glaridacris vogei	Indirect	A/P
Hunterella nodulosa	Indirect	A/P
Monobothrium sp.	Indirect	A/P
Truttaedacnitis truttae	Indirect	A
Raphidascaris acus	Indirect	A
Neoechinorhynchus cylindratus	Indirect	A/P
Pomphorhynchus bulbocolli	Indirect	A/P

drainage systems. Of the remaining nine, *Tetraonchus borealis*, *Truttaedacnitis truttae*, and *Raphidascaris acus* were recovered from *Thymallus arcticus*, which is restricted in its current distribution to the Arctic drainage. The other six, all from *Oncorhynchus tshawytscha*, were restricted to the Pacific drainage, i.e. along with their host.

Nine of the 26 species do not require intermediate hosts and their fish hosts occur in both systems. The probability of establishment of these species in the new environment following construction for the proposed diversion should be quite high. Two other parasites (*Ceratomyxa shasta* and *Tetraonchus borealis*) also have direct life cycles but their hosts are restricted to either the Arctic or the Pacific drainage. The success these taxa may have in becoming established will be dependent on the ability of the respective hosts to adapt in the new area or on the ability of the parasite to establish in other host species.

Of the 12 species with indirect life cycles, three from *Oncorhynchus tshawytscha* (*Brachyphallus crenatus*, *Genolinea oncorhynchi*, and *Lampritrema miescheri*) are known to be of marine origin and can be eliminated from consideration of possible parasite transfaunation. The hosts of eight of the remaining nine species occur in both drainages but the parasites are restricted in their distributions; if the current distributional patterns of these parasites are related to the presence or absence of intermediate hosts, transfaunation of the parasites will be dependent on the success these intermediate hosts will have in establishing themselves under new, postdiversion conditions.

Assessment of potential pathogens among the parasites with a disjunct distribution within the study area revealed several for which (1) pathological effects have been reported in the literature for either the specific parasite or related taxa or (2) host mortalities have been reported. Potential pathology was assessed on the basis of literature reports, since an evaluation of pathology per se was beyond the terms of reference of this study. However, we have found that there is reliable information of a general nature for establishing the level of pathology that might be expected within a parasite group.

Parasites for which pathological effects have been reported include six protozoans (*Chloromyxum granulosum*, *C. montschadskii*, *Cryptobia salmositica*, *Haemogregarina irkalukpiki*, *Pleistophora* sp., and *Trichodina* sp.), two cestodes (*Hunterella nodulosa* and *Monobothrium* sp.), and an acanthocephalan (*Pomphorhynchus bulbocolli*). The two species of *Chloromyxum* are included here, since reports indicate that other members of the genus are associated with necrosis of tissue and general debilitation of the host (Rogers and Gaines 1975). *Cryptobia salmositica* is known from all six species of *Oncorhynchus* and from many other species of freshwater teleosts on the Pacific coast, from northern California to British Columbia (Becker and Katz 1965). Woo (1979) reported that this species caused anemia, exophthalmia, abdominal distension, and splenomegaly in experi-

mentally infected *Salmo gairdneri*. Pathology of *Haemogregarina* in fishes is not well known, although damage to red blood cells and pathological changes in blood chemistry have been reported (Becker 1980). Species of *Pleistophora* have been incriminated in production of tumorlike cysts, while members of *Trichodina* have been reported to cause excess mucus production, debility, hyperplasia, and necrosis of the epidermis (Rogers and Gaines 1975). The three helminths belong to genera in which members have been shown to produce lesions at the site of attachment.

The only parasite for which host mortalities have been reported is *Ceratomyxa shasta*. *Ceratomyxa shasta* is known to cause a severe disease, ceratomyxosis, which involves the invasion of most tissues of the host (Wood 1974). Ceratomyxosis can produce high mortalities and for this reason is labeled a "certifiable" fish pathogen.

Environmental changes can have wide-ranging effects on various aspects of the biology of parasites. Since the extent of pathology is frequently determined by the intensity of infection and prevalence of parasitism, an alteration in the environment could result in greater deleterious effects on the host. Boyce and Yamada (1977) found that parasites can reduce the ability of fishes to withstand stress, and it has also been shown that parasites tend to affect hosts more readily when the host is under stress conditions. Other reports indicate that parasites introduced into new environments can have greater effects on their hosts, although the hosts are of the same species as those previously used; furthermore, the effects of parasites that are in the process of acquiring hosts of different species tend to cause more harm than in hosts with which they have had a longer period of association. Since there are only a few examples of what can occur in host–parasite relationships with changing environmental conditions, the potential consequences of introducing any of the parasites into new areas should be carefully considered.

Within the context of this study and referring to the 26 taxa that show disjunct distributions in the study area, those that have direct life cycles, have hosts that are currently in both drainage systems, and show relatively little host specificity will, in all probability, extend their geographical distribution and the range of fishes used as hosts following construction for the proposed diversion. In contrast, those parasites that were recovered from hosts that occur in only one of the drainage systems, have indirect life cycles, and are relatively host specific will probably have the least opportunity to become established in the new environment.

While not attempting to minimize the potential consequences related to transfaunation of any of the parasites, we have identified three forms (*Ceratomyxa shasta*, *Cryptobia salmositica*, and *Haemogregarina irkalukpiki*) as those that appear to pose the greatest threat to the fisheries resources of the area under consideration, i.e. both the study area and downstream areas that might be affected by transfaunation of the parasites. The latter two species are considered to be of less importance, primarily because they both require intermediate hosts and are reported to be less pathogenic. *Ceratomyxa shasta* is most problematical, since it appears to have a direct life cycle, is highly pathogenic, and could affect a very large geographic area, i.e. the entire Peace–Athabasca–MacKenzie river system.

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Dr Z. Kabata and Dr L. Margolis, Pacific Biological Station, identified copepods and confirmed identification of *Ceratomyxa shasta*, respectively. Dr F. Moravec, Institute of Parasitology, Czechoslovak Academy of Sciences, confirmed identifications of *Rhabdochona kisutchi* and *R. zacconis*. Dr J. Mackiewicz, State University of New York, Albany, identified the Caryophyllidae. Dr K. Molnar, Veterinary Research Institute, Hungarian Academy of Sciences, provided specimens of *Bothriocephalus* for comparative examination. Original studies, including field collection and laboratory analysis, were funded by the British Columbia Hydro and Power Authority as part of its environmental impact studies for the proposed McGregor River Diversion Project.

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Zinc, Manganese, and Strontium in Opercula and Scales of Brook Trout (*Salvelinus fontinalis*) as Indicators of Lake Acidification

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MOREAU, G., C. BARBEAU, J. J. FRENETTE, J. SAINT-ONGE, AND M. SIMONEAU. 1983. Zinc, manganese and strontium in opercula and scales of brook trout (*Salvelinus fontinalis*) as indicators of lake acidification. Can. J. Fish. Aquat. Sci. 40: 1685 – 1691.

Calcium, magnesium, zinc, manganese, and strontium were analyzed in opercula and scales of 148 brook trout (*Salvelinus fontinalis*) from three acidified and three nonacidified lakes in Laurentian Park north of Québec. In the acidified lakes, the content in manganese, zinc, and strontium is 1.6, 1.3, and 1.2 times higher than in the nonacidified lakes, whereas the concentrations in calcium and magnesium are not significantly different. A discriminant analysis correctly classifies more than 80% of all specimens. Furthermore, a cluster analysis based on zinc and magnesium concentrations in opercula is successful in grouping 73 and 78%, respectively, of fish from nonacidified and acidified lakes.

MOREAU, G., C. BARBEAU, J. J. FRENETTE, J. SAINT-ONGE, AND M. SIMONEAU. 1983. Zinc, manganese and strontium in opercula and scales of brook trout (*Salvelinus fontinalis*) as indicators of lake acidification. Can. J. Fish. Aquat. Sci. 40: 1685 – 1691.

Les concentrations en calcium, magnésium, zinc, manganèse et strontium ont été déterminées dans les écailles et les opercules de 148 truites mouchetées (*Salvelinus fontinalis*) provenant de trois lacs acidifiés et de trois lacs non acidifiés du Parc des Laurentides au nord de Québec. Dans les lacs acidifiés les concentrations moyennes de manganèse, zinc et strontium sont respectivement 1,6, 1,3 et 1,2 fois plus élevées que dans les lacs non acidifiés. Les concentrations en calcium et magnésium ne sont pas significativement différentes pour les deux groupes de lacs. Une analyse discriminante permet de classifier correctement plus de 80 % des spécimens dans leur groupe d'origine. Une analyse de groupement basée sur les concentrations en zinc et magnésium dans les opercules permet de regrouper avec succès 73 % et 78 % des poissons provenant des lacs acidifiés et des lacs non acidifiés.

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INORGANIC cations in water have been shown (Van Coillie et al. 1974; Van Coillie and Rousseau 1975) to affect the inorganic composition of scales in many fishes. This effect has been used to differentiate anadromous and freshwater populations of salmon (Bagenal et al. 1973) and whitefish (Moreau and Barbeau 1979), and has served to identify salmon stocks (Lapi and Mulligan 1981). The inorganic composition of bone structures of fishes could therefore reflect changes in the chemical characteristics of lake waters that result from acid precipitation. Many studies (Hall et al. 1980; Overrein et al. 1981; Jackson et al. 1980) have indeed shown that acid rain is responsible for an increase in dissolved metals, many of which could be included in the bone structures. Osmoregulation, well reviewed by Evans (1980) and Lahlou (1980), seems to be affected by acidification (Fromm 1980) and could also influence the mineralization of bone structures.

This study was conducted to look for the effect of lake acidification on metal composition of bone structures of brook trout (*Salvelinus fontinalis*). If we found distinctive metal concentrations in opercula and scales of fish from three acidified and three nonacidified lakes, then we could suggest using one or more of these metals as indicators of lake acidification.

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TABLE 1. Chemical characteristics of study lakes given as mean (SD) and range.

Parameter	Acidified lakes			Nonacidified lakes		
	Hamon	Monette	Ovide	Mignon	Noir	Opalin
pH	5.5 (0.54)	5.5 (0.43)	5.2 (0.70)	6.8 (0.44)	6.9 (0.45)	7.0 (0.43)
	4.7 ------ 6.0	4.6 ------ 5.9	4.2 ------ 6.1	6.2 ------ 7.6	6.3 ------ 7.6	6.4 ------ 7.7
Total alkalinity	1.8 (1.3)	1.9 (1.5)	1.9 (1.2)	6.9 (1.5)	11.4 (4.1)	13.1 (5.5)
mg/L $CaCO_3$	0.1 ------ 3.0	0.7 ------ 2.2	0.1 ------ 3.4	5.0 ------ 8.6	6.5 ------ 16.0	7.0 ------ 19.2
Calcium	1.4 (0.4)	1.3 (0.2)	1.5 (0.4)	2.2 (0.3)	3.1 (0.8)	3.5 (1.1)
mg/L	0.8 ------ 1.9	1.0 ------ 1.6	1.0 ------ 2.0	2.0 ------ 2.7	1.3 ------ 3.9	1.8 ------ 4.8
Sulfates	3.0 (1.0)	2.9 (0.8)	3.9 (1.2)	2.4 (0.5)	2.2 (0.6)	2.1 (0.6)
mg/L	2.0 ------ 5.0	2.0 ------ 4.4	3.0 ------ 6.3	2.0 ------ 3.0	1.5 ------ 3.5	1.5 ------ 3.2
HCO_3/SO_4[a]	0.57	0.63	0.47	2.76	4.97	5.98
Conductivity	18.0 (2.0)	15.0 (1.0)	21.0 (4.0)	24.0 (2.0)	34.0 (6.0)	38.0 (8.0)
μS/cm	15 ------ 19	14 ------ 17	17 ------ 27	22 ------ 26	21 ------ 40	25 ------ 46
Magnesium	0.4 (0.1)	0.3 (0.1)	0.4 (0.1)	0.8 (0.2)	1.2 (0.2)	1.3 (0.3)
mg/L	0.2 ------ 0.5	0.2 ------ 0.4	0.2 ------ 0.5	0.7 ------ 1.0	0.7 ------ 1.4	0.8 ------ 1.6
Zinc	The majority of samples in all lakes contained less than 10 μg/L					
μg/L						
Manganese	30 (10)	40 (10)	30 (10)	30 (20)	40 (30)	90 (60)
μg/L	10 ------ 50	10 ------ 50	20 ------ 50	10 ------ 70	10 ------ 80	10 ------ 140

[a]From concentrations in mmol/L.

Materials and Methods

Brook trout, *Salvelinus fontinalis*, came from six lakes in Laurentian Park, Québec. The park is located in the Canadian Shield and receives between 1100 and 1500 mm of annual precipitation (Gagnon 1970) with approximately 13.5 $kg \cdot ha^{-1} \cdot a^{-1}$ of sulfate (Anon. 1981). The six lakes were chosen among 158 lakes for which chemical data, gathered in March 1981 by the ministère de l'Environnement du Québec, were available. Three criteria were used to select the acidified lakes: pH and calcium values according to Henriksen's model (1979), molar ratio of HCO_3/SO_4 less than 1.0 and total alkalinity less than 2 mg/L $CaCO_3$. Three other lakes, considered nonacidified according to these criteria, were chosen in the vicinity of the acidified lakes. One nonacidified lake, Lake Mignon, is less mineralized than the two other lakes of the group. All six lakes are headwater lakes of small area (19–29 ha) located at an altitude varying between 775 and 850 m and all six watersheds are free of any human activity apart from occasional angling and hunting. The mean values and the range of some chemical parameters of their surface waters have been compiled in Table 1 from monthly measurements made between October 1981 and June 1982.

During September and October 1981, 148 trout (73 females and 75 males) were caught using gill nets. More than 90% of all fish captured were aged between 2 and 4 yr. The scales and the opercula were immediately removed and kept dry at 4°C. Prior to the chemical analysis, the scales were soaked for 12 h in a KOH solution (1%), rinsed with distilled water and dried at room temperature. Thin skin covering the opercula was removed before chemical analysis. A narrow radial band of opercular bone weighing between 5 and 10 mg was cut from the opercula with a stainless steel scalpel. An appropriate number of scales was taken to make up 5–10 mg.

Opercula sections and scales were digested in $HClO_4$ and HNO_3 and analyzed for calcium, magnesium, and strontium according to the methods previously described (Moreau and Barbeau 1979). Zinc and copper in the solutions of digestion were analyzed by atomic absorption at 214 and 325 nm, respectively. Manganese and aluminum in the solutions were determined in the graphite furnace by atomic absorption at 280 and 309 nm, using standard conditions. Analysis of total operculum was performed on selected samples from the six lakes for control purposes and to increase the analytical response for aluminum and copper as these two metals are present at very low concentrations.

Of all analytical data, less than 2% were rejected on the basis of abnormal values for magnesium and zinc. These cases occurred only in scales with total weight less than 5 mg.

Data were submitted to a Komolgorov–Smirnov test for goodness-of-fit (Sokal and Rohlf 1981). Subsequent use of parametric or nonparametric univariate tests stems from the results of this procedure.

Comparisons of mean metal concentrations among fish from the different lakes, for both scales and opercula, were done by means of a one-way analysis of variance (Sokal and Rohlf 1981) or Kruskal–Wallis one-way analysis of variance by ranks (Siegel 1956). Homogeneity of variances was verified by means of Bartlett's test whenever parametric tests were to be used (Sokal and Rohlf 1981). Multiple comparisons among means were done using Duncan's multiple range test.

Bartlett's test, analysis of variance, Kruskal–Wallis analysis of variance by ranks, and Duncan's multiple range test were performed with programs from SACADOS (Boudoux and Bonenfant 1979). A cluster analysis based on Gower's similarity coefficient (Legendre and Legendre 1979) and using complete linkage clustering was done by means of a program from NT–SYS (Rohlf et al. 1974). Finally, a Kolmogorov–Smirnov test for goodness-of-fit and the discriminant analysis were carried out using programs from SPSS (Nie et al. 1975).

TABLE 2. Inorganic composition of opercula of brook trout ($\bar{x}$ = mean value; SD = standard deviation; C.V. = coefficient of variation).

Lake		Metal Ca mg/g	Mg mg/g	Zn μg/g	Mn μg/g	Sr μg/g	Ratio Mg/Zn
Hamon	$\bar{x}$	150.8	2.90	362	41.4	301	8.51
n = 29	SD	(25.6)	(0.30)	(89)	(8.9)	(50)	(2.38)
Monette		160.9	2.79	403	48.9	338	7.27
n = 26		(20.7)	(0.28)	(91)	(14.3)	(34)	(1.81)
Ovide		136.9	2.34	394	37.9	369	6.45
n = 16		(20.5)	(0.33)	(88)	(7.8)	(44)	(2.94)
Pooled	$\bar{x}$	151.4	2.73	384	43.4	330	7.59
acidified lakes	SD	(24.2)	(0.37)	(90)	(11.7)	(50)	(2.44)
n = 71	C.V.	15.32	13.61	15.99	26.98	23.51	
Mignon		154.6	3.09	285	33.8	261	12.61
n = 24		(17.2)	(0.30)	(117)	(12.2)	(35)	(5.85)
Noir		152.1	2.85	299	23.7	276	9.94
n = 23		(21.8)	(0.33)	(63)	(8.1)	(38)	(2.30)
Opalin		158.5	3.09	284	24.8	279	11.80
n = 30		(27.1)	(0.34)	(75)	(9.1)	(32)	(4.34)
Pooled	$\bar{x}$	155.4	3.02	289	27.3	273	11.50
nonacidified lakes	SD	(22.7)	(0.34)	(87)	(10.8)	(35)	(4.50)
n = 77	C.V.	12.99	11.37	14.58	39.47	29.29	

TABLE 3. Inorganic composition of scales of brook trout ($\bar{x}$ = mean value; SD = standard deviation; C.V. = coefficient of variation).

Lake		Metal Ca mg/g	Mg mg/g	Zn μg/g	Mn μg/g	Sr μg/g	Ratio Mg/Zn
Hamon	$\bar{x}$	105.8	2.18	221	39.7	287	10.48
n = 29	SD	(21.4)	(0.60)	(64)	(8.9)	(38)	(3.91)
Monette		117.7	2.07	258	50.4	313	8.44
n = 26		(29.6)	(1.15)	(90)	(17.6)	(52)	(4.09)
Ovide		114.6	2.03	269	49.0	383	7.81
n = 16		(11.5)	(0.60)	(45)	(10.7)	(54)	(3.11)
Pooled	$\bar{x}$	112.1	2.11	246	45.7	318	9.13
acidified lakes	SD	(23.5)	(0.83)	(73)	(13.9)	(60)	(3.94)
n = 71	C.V.	18.79	39.6	30.97	30.33	29.89	
Mignon		127.7	2.28	163	35.2	264	18.04
n = 24		(37.5)	(0.76)	(66)	(14.0)	(49)	(14.58)
Noir		114.2	2.02	186	26.4	295	10.84
n = 23		(20.8)	(0.59)	(27)	(10.9)	(48)	(2.60)
Opalin		103.0	2.07	177	26.1	257	11.88
n = 30		(18.4)	(0.65)	(33)	(8.8)	(48)	(3.99)
Pooled	$\bar{x}$	114.0	2.12	175	29.0	271	13.49
nonacidified lakes	SD	(28.0)	(0.67)	(45)	(11.9)	(51)	(9.06)
n = 77	C.V.	18.69	31.48	29.58	40.95	25.58	

Results

The concentrations in scales and opercula, for magnesium, zinc and manganese do not differ significantly (t-test: $P \leq 0.05$) from males to females. Strontium is slightly but significantly ($P \leq 0.05$) higher in females of the acidified lakes. As the sex ratio is approximately 1 in both groups of lakes, these small differences have no real meaning and no distinction was made between males and females. Aluminum and copper concentrations lie close to the practical limit of determination (< 45 and < 2 μg/g, respectively), even with complete opercula; these data have not been further analyzed.

Mean concentrations of calcium, magnesium, zinc, manganese, and strontium are presented in Table 2 for the opercula, and in Table 3 for the scales. In scales, the concentrations are lower than in opercula, with the exception of manganese. In all cases, the variability in concentrations is higher in scales than in opercula, as shown by the coefficients of variation (Table 2 and 3). When the analytical data are pooled under acidified and nonacidified groups, zinc, manganese, and strontium concentrations are higher in scales and opercula of trout from the acidified lakes ($P \leq 0.05$), whereas

TABLE 4. Multiple comparisons among means from the six lakes (Duncan's test) for the different components of opercula and scales. The lakes grouped by a continuous line show no significant differences among them ($P \leq 0.05$). A single factor analysis of variance by ranks (Kruskal–Wallis test) was used when no-normality was encountered.

Sr	Opercula	Mi	No	Op	Ha	Mo	Ov
	Scales	Op	Mi	Ha	Mo	No	Ov
Mg	Opercula	Ov	Mo	No	Ha	Mi	Op
	Scales	No	Ov	Op	Mo	Ha	Mi
Ca	Opercula	Ov	Ha	No	Mi	Op	Mo
	Scales	Op	Ha	No	Ov	Mo	Mi
Mn	Opercula	No	Op	Mi	Ov	Ha	Mo
	Scales	Kruskal–Wallis $P \leq 0.05$					
Zn	Opercula	Op	Mi	No	Ha	Ov	Mo
	Scales	Mi	Op	No	Ha	Mo	Ov

neither calcium nor magnesium concentrations are significantly different (*t*-test: $P > 0.05$).

TOTAL DATA

A comparative study of mean values for each lake (Table 4) shows that zinc and strontium present differences between acidified and nonacidified lakes with no overlapping of the two groups. Manganese is higher in opercula of trout from the acidified lakes but not always significantly. In scales, there is more overlapping of the groups and only zinc shows a clear difference.

Because these overlappings could invalidate the a priori classification of lakes, a cluster analysis was done on all trout. For opercula, three groups are distinguished at a level of similarity of 0.57. The first group is composed of 79% of trout from the nonacidified lakes, the second group is made of 92% of trout from the acidified lakes and the third group is intermediate with 58% of samples from the acidified lakes (Fig. 1). The two first groups contain 77% (114/148) of all trout. A similar analysis using scales shows that, with the same level of similarity, three groups are also distinguishable. The first group contains 76% of specimens from the nonacidified lakes, the second group is made of 80% of trout from the acidified lakes and the third group is intermediate with 71% of trouts from the nonacidified lakes. The first two groups hold 80% (118/146) of all specimens and only two trout from Lake Noir cannot be included in one of the three groups. The high percentage of correctly classified trout validates the initial classification of lakes into two groups.

To find the variables that characterize these two groups, a discriminant analysis was performed on trout from these two groups using the metals in the opercula as discriminant variables. It was successful in classifying correctly 84% of the fish in their original group. The percentage of correctly classified fish from the acidified lakes was 80% compared to 88% for fish from the nonacidified lakes. A similar analysis was applied to the data of scales. Even though the percentages are different from those of the opercula and the order of major discriminant variables is not the same (Table 5), the percentage of correctly classified trout is similar in the analysis of groups, 83% (Table 6). A discriminant analysis applied to the six lakes gives a first function explaining 79% of the variance and a second function related to 18% with magnesium, manganese, and strontium as the main discriminant variables.

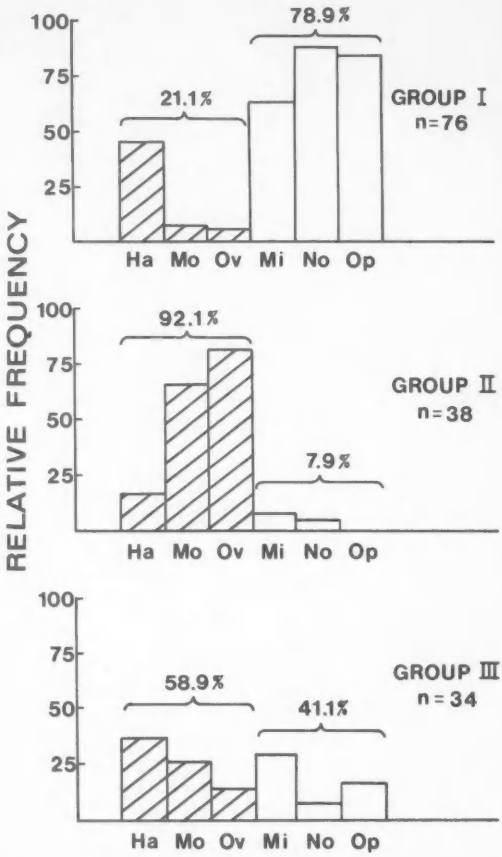

FIG. 1. Group distribution from cluster analysis based on calcium, magnesium, strontium, manganese, and zinc concentrations in opercula (Lakes HAmon, MOnette, OVide, MIgnon, NOir, OPalin; acidified lakes under slashed lines).

REDUCED DATA

A cluster analysis done with only zinc and magnesium from opercula shows that three groups exist at a similarity level of 0.59. The first group has more than 73% of trout from the nonacidified lakes, the second group contains 78% of specimens from the acidified lakes and the third group holds only 7% of the total population.

TABLE 5. Standardized discriminant function coefficients for the discriminating variables in opercula and scales of trout and identification functions for opercula of the two groups of lakes.

Opercula		Scales	
Variable	Coefficient	Variable	Coefficient
Manganese	0.627	Manganese	0.659
Magnesium	−0.579	Zinc	0.594
Strontium	0.458	Calcium	−0.387
Zinc	0.335	Strontium	0.286
Calcium	0.004	Magnesium	−0.151

Identification function of group 1 (acidified)
−53.986 + 1.398(Sr) + 1.778(Mg) − 0.001(Ca) + 0.144(Mn) + 0.168(Zn)
Identification function of group 2 (nonacidified)
−49.826 + 1.153(Sr) + 2.155(Mg) − 0.001(Ca) + 0.014(Mn) + 0.080(Zn)

TABLE 6. Classification results of the discriminant analysis for opercula and scales of trout from the two groups of lakes.

	Percentage of correctly classified trout			
	Acidified		Nonacidified	
Group	Opercula	Scales	Opercula	Scales
Acidified $n=71$	80.3% $n=57$	77.5% $n=55$	19.7% $n=14$	22.5% $n=16$
Nonacidified $n=77$	11.7% $n=9$	11.7% $n=9$	88.3% $n=68$	88.3% $n=68$

Percentage of grouped trout correctly classified (opercula): 84.5
Percentage of grouped trout correctly classified (scales): 83.1

Discussion

The pooled inorganic composition of scales and opercula from brook trout in the acidified lakes is different from that observed in specimens of the nonacidified lakes (Table 2 and 3). The differences are most important for manganese, zinc, and strontium, with concentrations respectively 1.6, 1.3, and 1.2 times higher in scales and opercula of the acidified lakes.

The average calcium concentrations in these trout tissues do not differ from one type of lake to another. The same is true with magnesium in scales whereas only a 10% variation can be observed in opercula of the two groups of lakes. Both calcium and magnesium remain practically constant in scales and opercula, in spite of important variations in the concentrations of these two cations in the different waters. Fromm (1980) suggests that, under acid stress, H^+ ions may replace Ca^{2+} ions in gills, producing an increased permeability for all ions with a resulting loss of these ions. This may be helpful in explaining observations by Beamish et al. (1975), Beamish (1976), and by Lockhart and Lutz (1977) who found that females in acid waters do not show the normally expected increase of calcium in serum during the reproduction period. Such a metabolic disruption could be one of the reasons of the accelerated disappearance of fish in waters of low pH and low calcium content (Wright and Snekvik 1978; Brown 1981). However, such a loss from serum does not seem to result in a similar loss of calcium in bone structures as indicated by the absence of decalcification in ribs of *Catostomus commersoni* in acidified waters (Lockhart and Lutz 1977) and by our own results. Fraser and Harvey (1982) also found no decalcification in ribs or opercula of *Catostomus commersoni* in acidified waters but observed that the calcium content in vertebrae was much lower in fish from acid lakes. No explanation was given for these differences.

Zinc concentrations in trout are markedly different in the two groups of lakes for both scales and opercula. The values pertaining to Lake Mignon, which is less mineralized than the two other nonacidified lakes, are indistinguishable from these two lakes. It seems therefore that opercula zinc concentrations would follow the pH values, being mobilized more strongly in acidified waters as it dissolves more readily in such waters (Schindler 1980). In nonacidified lakes of pH greater than 6.0, the zinc concentration remains under 10 μg/L (Beamish 1976; Yan et al. 1979), varies between 15 and 80 μg/L in lakes of pH less than 5.3 (Henriksen and Wright 1977; Adamski and Michalski 1975) and presents a mean value of 15 μg/L in lakes of pH 5.6−6.0 (Dillon et al. 1979; Yan et al. 1977). These values show that higher zinc concentrations are expected in acidified waters such as our three acidified lakes, even though our measured dissolved concentrations in surface waters do not apparently differ (Table 1).

The average concentrations of manganese in trout from the two groups of lakes are very different but the values related to Lake Mignon are higher than those of Lake Noir and Lake Opalin and close to those of an acidified lake. Such increases in manganese concentrations have already been observed in tissues of white suckers by Lockhart and Lutz (1977) and by Fraser and Harvey (1982). Manganese, which is present in sediments and dry or wet precipitation, is more soluble in acidified waters, going from an average value of 3 μg/L in lakes of pH greater than 6.0 (Beamish 1976) to a range of values between 50 and 400 μg/L in lakes of pH less than 5.3 (Beamish 1976; Dickson 1975, 1980). In contrast to zinc, dissolved manganese concentrations depend on the redox conditions in water and thus vary with depth and period of the year. In our study, the measured surface concentrations remain low in both groups of lakes (Table 1). In view of the importance of the redox chemistry of manganese on its level in solution, of its low content in scales and opercula and of the intermediate values measured in Lake Mignon's samples, this variable does not appear to reflect clearly the distinct acidity of our two groups of lakes.

The average strontium concentrations are higher in scales and opercula of trout from the acidified lakes and Lake Mignon does not differ from the two other nonacidified lakes. This parameter follows the same trend as zinc but the differences are not as pronounced. With less than 10 μg/L of dissolved strontium in lake waters, its increased availability in acidified waters is speculative. Because of its low content, the difficulty of accurate determination and its relatively low enrichment in samples from the acidified lakes, strontium ranks second to zinc as a distinctive variable.

Even though it has been suggested that calcium concentration in water may affect the uptake of trace metals

(McFarlane and Franzin 1980) our data show that only manganese correlates significantly ($P < 0.05$) with calcium (Spearman's rank test: $r = 0.94$). Furthermore, trout from Lake Mignon, which has the lowest calcium concentration of the nonacidified lakes (2.2 vs 3.1 and 3.5) presents zinc and strontium concentrations similar to the other two nonacidified lakes. It has also been suggested that osmoregulation which plays an important role on the concentration of trace cations in scales or opercula could be affected by the amount of H^+ ions. Unfortunately, the effect of the pH on the absorption and elimination of cations has only been well studied for sodium (Evans 1975, 1980; Leivestad et al. 1976, 1980; McWilliams and Potts 1978; Packer and Dunson 1970). The urophysis of the trout from our acidified lakes seem to be histologically more active (G. Chevalier, Département des Sciences biologiques, U.Q.A.M., Montréal, personal communication), a fact that could perhaps be related to a stronger absorption of cations (Fryer et al. 1978; Chan 1975). Whatever the physiological mechanism, the concentrations of zinc, strontium, and manganese appear to be useful as indicators of increased acidification, as they were successful in correctly classifying more than 80% of the trout in the lakes under study.

By using the identification functions given in Table 5, it is possible to compare new data and eventually relate fish to acidified or nonacidified lakes. Magnesium and zinc concentrations may provide the same information, as shown by our cluster analysis with these two variables. Even zinc concentrations alone appear to be sufficient in order to distinguish the fish from acidified and nonacidified lakes, at least in our case. To avoid misinterpretation, which could result from the presence of noncationic material in scales or opercula such as organic constituents or debris, we suggest that magnesium be analyzed together with zinc. Any magnesium value far away from the mean should render the zinc value suspect. The chemical analysis can be performed on either scales or opercula, the latter being preferred when no cleaning treatment is wanted or when the scales are very small.

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Nutrient Flux onto the Labrador Shelf from Hudson Strait and its Biological Consequences

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Fish abundance, based upon commercial fish catches and numbers of fish-feeding birds, is shown to increase southward along the Labrador Shelf from Hudson Strait. Also, yearly abundance of Labrador Atlantic cod (*Gadus morhua*) using virtual population analysis is shown to be closely correlated with salinity changes at Station 27 off St. John's, Newfoundland. We suggest these observations are related to physical oceanographic events originating within Hudson Strait. Analysis of available data indicates nutrient enrichment of the surface waters through physical mixing in Hudson Strait. These waters are carried by the residual circulation onto the northern Labrador Shelf. Our interpretation of the southward increase in fish abundance is that fish production develops downstream of the area of nutrient injection due to the southward flow of the Labrador Current coupled with the time required for food chain development. The yearly variation of cod is interpreted as arising from the variation of the nutrient supply, which is itself correlated with salinity. The fresh water discharge into Hudson Bay which eventually flows out through Hudson Strait and onto the Labrador Shelf appears to suppress mixing and hence years of higher discharge would tend to decrease the nutrient supply.

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L'abondance des poissons, fondée sur les prises commerciales et le nombre d'oiseaux ichtyophages, augmente depuis le détroit d'Hudson vers le sud le long du plateau du Labrador. En outre, l'analyse de population virtuelle indique que l'abondance annuelle de la morue (*Gadus morhua*) du Labrador est en étroite corrélation avec les changements de salinité à la station 27 au large de St-Jean (Terre-Neuve). Ces observations seraient reliées aux phénomènes océanographiques physiques prenant naissance dans le détroit d'Hudson. Selon les données existantes, il y a enrichissement en substances nutritives des eaux de surface par un processus de mélange physique dans le détroit d'Hudson. Ces eaux sont transportées par circulation résiduelle sur la portion septentrionale du plateau du Labrador. Nous interprétons cette augmentation vers le sud de l'abondance des poissons comme étant le résultat d'une production qui se développe en aval de la zone d'injection de substances nutritives sous l'influence de l'écoulement vers le sud du courant du Labrador couplé à la période requise pour le développement de la chaîne alimentaire. La variation annuelle de l'abondance de la morue serait due à la variation des apports de nutriments, eux-mêmes dépendant de la salinité. Le débit d'eau douce dans la baie d'Hudson qui en sort éventuellement par le détroit d'Hudson

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et se répand sur le plateau du Labrador semble empêcher le mélange et, par conséquent, dans les années de fort débit, les apports de substances nutritives auraient tendance à diminuer.

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COMMERCIAL fish catches on the continental shelf off Labrador and Newfoundland suggest moderately high productivity within these regimes. Although catches off northern Labrador are low, southern Labrador and northern Newfoundland (North Atlantic Fisheries Organization (NAFO) Subareas 2J, 3K; see Fig. 1 for NAFO subareas) yielded an annual average of 2.5 t km^{-2} and the Grand Banks (NAFO Subareas 3L, N, O) about 2 t km^{-2} between 1961 and 1970. These compare with 4 t km^{-2} for New England (NAFO Subarea 5) and nearly 5 t km^{-2} for the North Sea (ICES Areas IIIa, IV).

Little is known about the primary production of the Labrador–Newfoundland Shelf but nutrient supply is certainly an important underlying influence during the summer. This paper examines, with available data, allochthonous nutrient sources to the Labrador Shelf and their effect on the biological production of the Shelf. The role of the mean circulation and of the low salinity water originating from Hudson Bay on the biology of the Shelf region are also considered. The physical oceanography of the Labrador Shelf and the Hudson Strait–Baffin Island Shelf region to the north has been discussed by Smith et al. (1937), Dunbar (1951, 1958), Campbell (1958), and Kollmeyer et al. (1967) and more recently by LeBlond et al. (1981), LeBlond (1982), and Lazier (1982). The general circulation is southward (see insert in Fig. 1). We will refer to the flow north of Hudson Strait as the Baffin Land Current following Smith et al. (1937). The flow south of the Strait is known as the Labrador Current.

Nutrient Supply to the Labrador Shelf

The uptake of nutrients from seawater is an essential requirement for primary production. In Arctic and temperate latitudes depletion of the available nutrients by the phytoplankton during the spring or early summer bloom generally limits algal growth through the summer and fall unless new sources of nutrients become available. On the Labrador Shelf the possible nutrient sources for primary production during summer, aside from in situ regeneration, are the surface waters offshore through cross-shelf mixing, the deep (> 50 m) waters on the Shelf through vertical mixing and the surface waters to the north by advection. Although large scale eddies have been observed off the continental slope of Labrador (LeBlond 1982) they do not appear to produce significant horizontal exchanges of water such as has been observed further to the south when Gulf Stream eddies impinge upon the Scotian Shelf off Nova Scotia (Smith 1978). Indeed, cross-shelf mixing as well as vertical mixing appear to be of minor importance on the Labrador Shelf. Analysis of historical temperature and salinity data (Lazier 1982) shows, on average, summer temperatures differ by less than 1°C and salinities by 0.5 (using the Practical Salinity Scale 1978) between the northern and southern halves of the Labrador Shelf. Lazier noted the differences lay within one standard deviation and may not even be real. This lack of a distinct alongshore gradient in temperature and salinity indicates little or no cross-shelf mixing or vertical mixing on the shelf. It would appear one must look to advection and the origins of the Labrador Shelf water for any significant contribution of nutrients.

The T–S characteristics of the water on the Labrador Shelf are formed in Hudson Strait (Dunbar 1951; Kollmeyer et al. 1967) from mixing of the cold southward moving Baffin Land Current, the warm West Greenland waters and the eastward outflow carrying low salinity water from Hudson Bay and Foxe Basin. The West Greenland waters, so named since they originate from the West Greenland Current, are the offshore waters along the Baffin Island and Labrador Shelves. The effect of the mixing in Hudson Strait can be seen from the difference in the T–S properties between the water to the north of the Strait on the Baffin Island Shelf and to the south on the Labrador Shelf (Fig. 2). The data were collected in July–August 1965 by the United States Coast Guard (Kollmeyer et al. 1967) along transects G (Stn. 9477–9482) and C (Stn. 9438–9448) and in October 1977 during the C.S.S. *Hudson* cruise 77-029 (J. Lazier, Bedford Institute of Oceanography, personal communication) along transects A (Stn. 1–8) and B (Stn. 23–30). The transect positions are shown in Fig. 1. During 1965 the temperature of the subsurface minimum (~100 m) increased by 1–2°C and its salinity decreased by 0.5–1 (Practical Salinity Scale 1978) from north to south across the entrance to Hudson Strait (Fig. 2). In 1977 the temperature minimum layer (0 to −1°C) observed north of Hudson Strait was absent south of the Strait with minimum temperatures (1°C) at the surface (Fig. 2) as was also noted by Lazier (1982). The lower salinities in 1965 south of the Strait reflect the greater influence of outflow from Hudson Bay and Foxe Basin during July and August.

It is evident from the chemical data in Kollmeyer et al. (1967) that the mixing within Hudson Strait also enriches the near surface nutrient levels, the nutrients becoming available biologically as the water is transported out of the Strait and then southward along the Labrador Shelf by the mean circulation. We will consider only nitrates in the following discussion. These were found by Grainger (1975) to be the limiting nutrient to primary production during the summer from studies conducted within Frobisher Bay immediately north of the eastern entrance to Hudson Strait. Using data from Kollmeyer et al. (1967) nitrate concentrations, averaged over the top 50 m of the water column and across the width of the shelf, showed an increase from 1.5 μmol/L on the Baffin Island Shelf (line G) to 3.4 μmol/L on the northern Labrador Shelf (line C). During the same period nitrate concentrations at the eastern entrance to Hudson Strait (Kollmeyer et al. 1967, line D, stn. 9451–9458) had a depth-averaged mean of 4.6 μmol/L which, together with the known mean circulation, is consistent with the idea of Hudson Strait as the source of the high nitrates on the northern Labrador Shelf. Nitrate enrichment on the Labrador Shelf

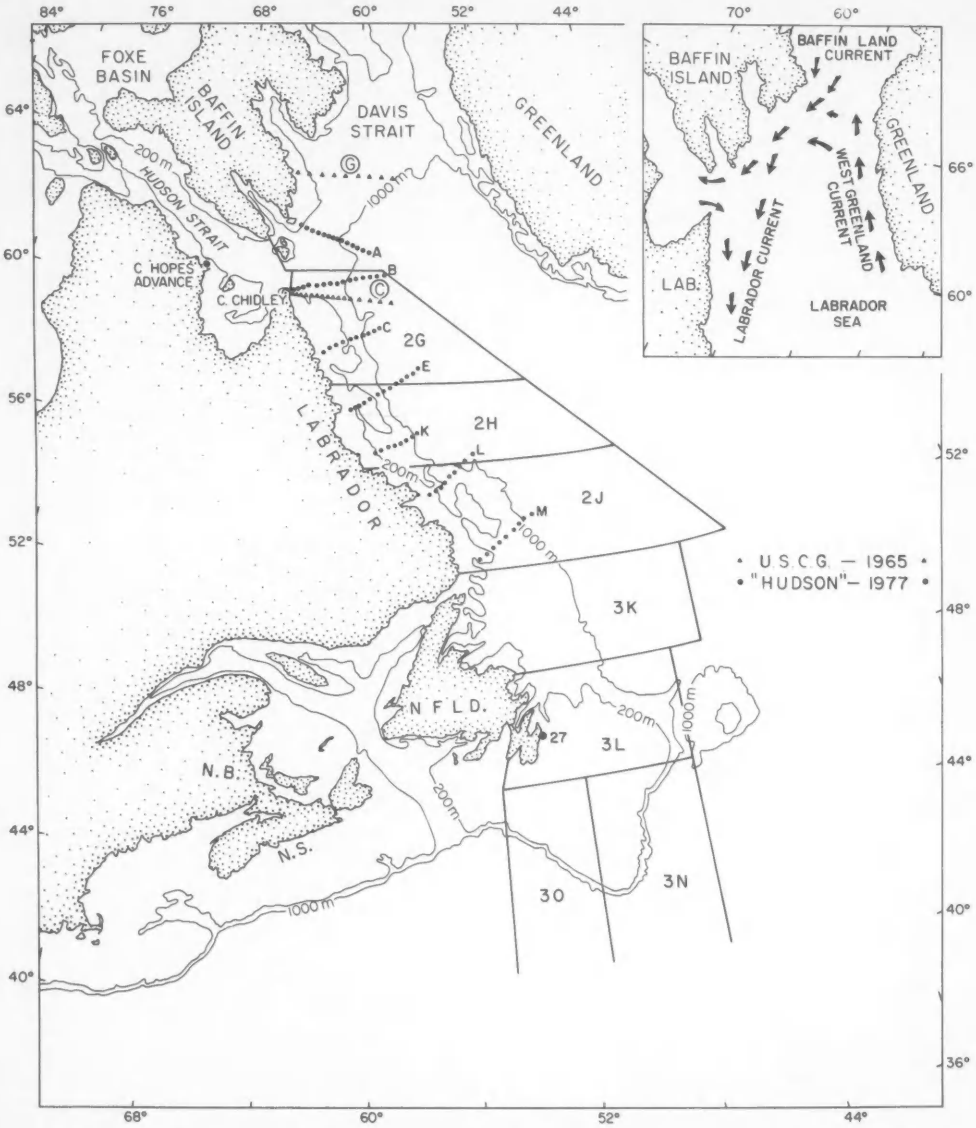

FIG. 1. The Labrador Shelf showing the Northwest Atlantic Fisheries Organization (NAFO) Subarea boundaries together with the stations occupied during C.S.S. *Hudson* cruise in October 1977 and the U.S. Coast Guard Ice Patrol cruise in July–August 1965. The insert, taken from LeBlond et al. (1981), shows the major ocean surface currents.

relative to the southern Baffin Island Shelf was also found during the *Hudson* cruise in October 1977. At that time average nitrate concentrations were 1.9 μmol/L off Baffin Island (line A) and 5.4 μmol/L off northern Labrador (line B). This increase is also shown in the plots of NO_3 vs σ_t (Fig. 3). In the near surface waters ($\sigma_t \leq 26.5$) the nitrate concentrations on a given σ_t surface were higher south of Hudson Strait (lines B, E, K) than those north of the Strait (line A). No data

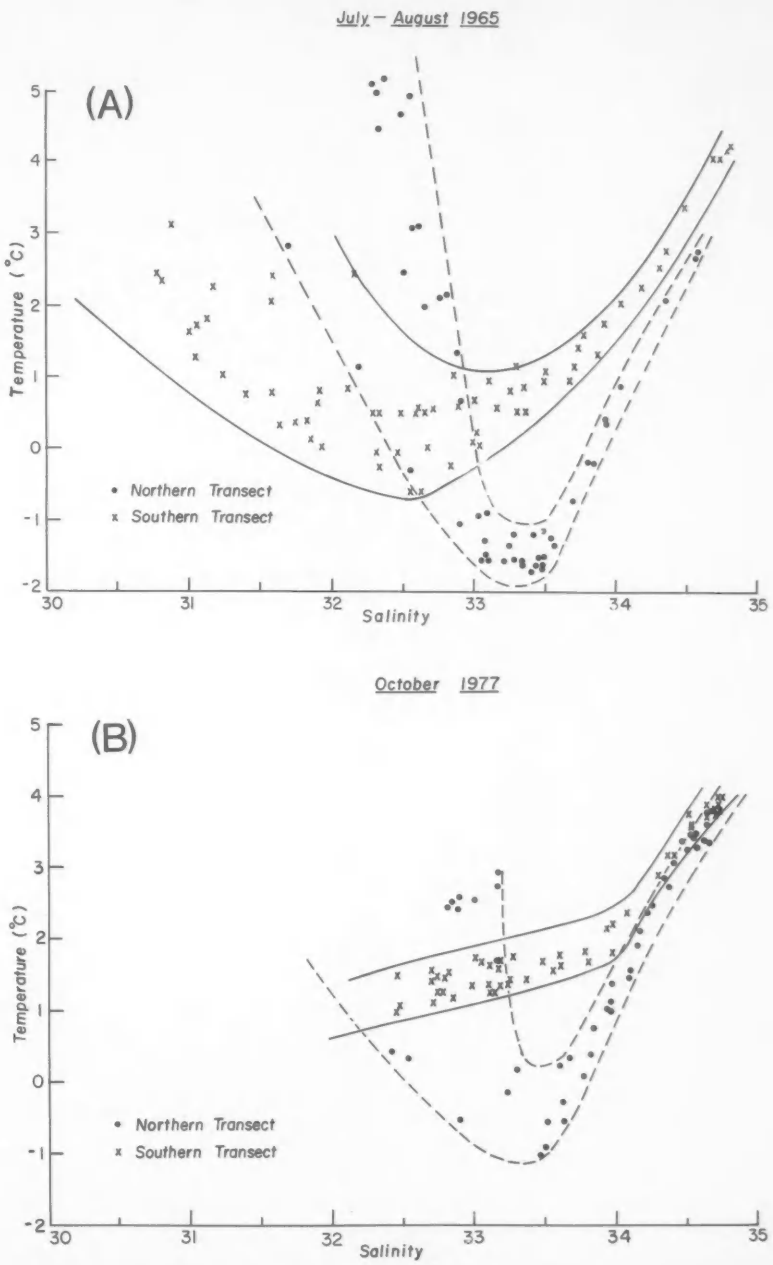

FIG. 2. T–S diagrams for stations north and south of Hudson Strait for (A) July–August 1965 and (B) October 1977.

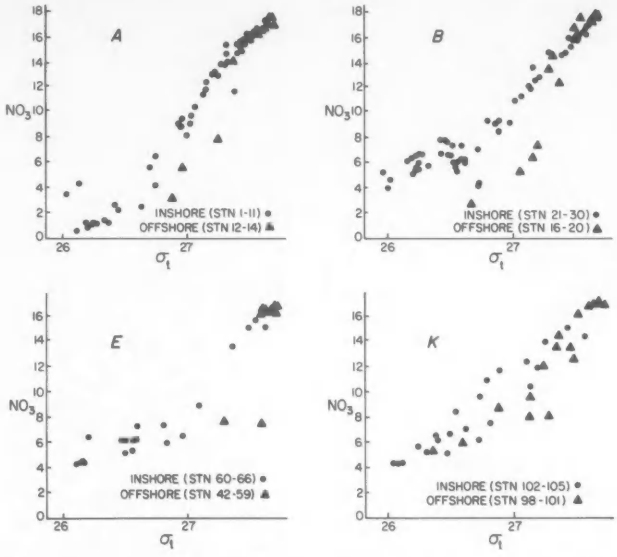

FIG. 3. Nitrate (NO_3) versus density (σ_t) plots for transects A, B, C, and D occupied during October 1977. The transect locations are shown in Fig. 1.

TABLE 1. Water properties of Labrador Shelf and its constituents during October 1977.

Property	Fresh-water	Baffin Surface	Polar	West Greenland	Labrador
Temperature (°C)	4.0	2.5	−1.0	4.0	1.5
Salinity	0	33.0	33.5	34.8	33.0
Nitrate (μmol/L)	0	1.5	9	17	7

were collected within Hudson Strait during the October 1977 cruise.

Differences in the surface nitrates did occur between the 1965 and 1977 cruises. The July–August 1965 data showed low surface nitrates (<1 μmol/L) except in the immediate vicinity of Hudson Strait. In October 1977 the surface values of all stations on the Labrador Shelf were high, varying from 3 to 6 μmol/L but, in contrast, measurements taken on the Baffin Island Shelf 2 d earlier showed low values near-surface (<2 μmol/L). Assuming no great dissimilarities in the dynamics or the marine climate between 1965 and 1977, these differences can be interpreted as reflecting a relatively high biological activity, using up surface nutrients on the Shelves in summer (July 1965) but a slowing or cessation of activity in autumn (October 1977). Nutrient advection from Hudson Strait would account for the relatively high surface values on the Labrador Shelf in October 1977 as compared to the Baffin Island Shelf where only in situ regeneration and diffusion would be occurring.

Before considering the biological effect of this nutrient flux onto the northern Labrador Shelf we shall discuss further the mixing in Hudson Strait. The waters that are mixed within the Strait are derived from four sources, the fresh water runoff into Hudson Bay, Baffin Land Current surface waters, polar waters (Dunbar 1951), and West Greenland waters. Polar waters are the subsurface waters in the Baffin Land Current and the outflow from Foxe Basin and Hudson Bay into Hudson Strait. To determine their approximate relative proportions in the makeup of the resultant mixture, i.e. the inshore Labrador Shelf waters, characteristic temperature, salinity and nitrate values were determined from the October 1977 data for the Shelf waters and its four constituents (Table 1). Four simultaneous equations were then written by assuming conservation of these water properties together with the conservation of volume. Solving these equations, the Labrador Shelf water at that time consisted of 42% surface waters of the Baffin Land Current, 37% polar waters, 19% West Greenland waters, and 2% runoff. Combining these results with Table 1 it can be seen that the high nutrient levels found on the Labrador Shelf were derived principally from polar and West Greenland waters.

Several hypotheses have been advanced to account for the large-scale mixing in Hudson Strait. Bottom generated tidal mixing near the eastern entrance was suggested by Iselin

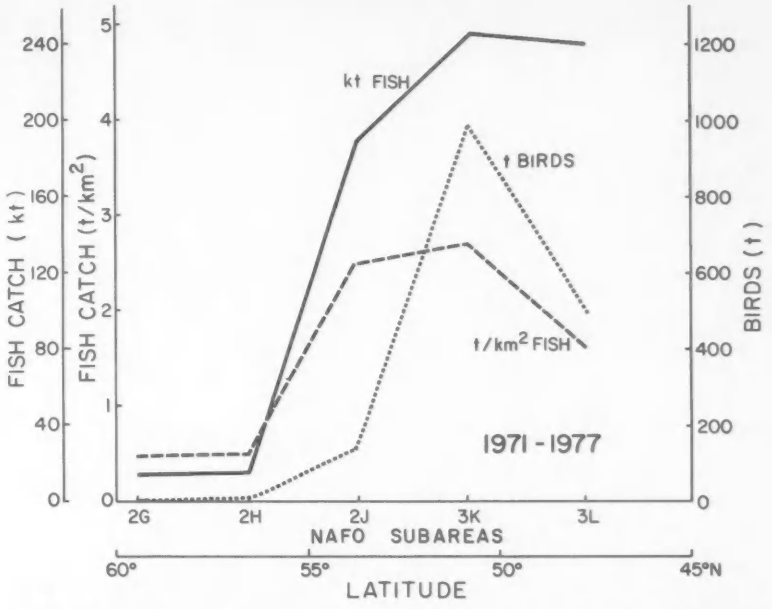

FIG. 4. Fish catch, fish catch per unit area, and bird abundance plotted as a function of longitudinal distance along the Labrador–Newfoundland Shelf.

(1927), Dunbar (1951), Campbell (1958), and Griffiths et al. (1981). The tides in Hudson Strait are large with tidal sea surface elevations of 5 to 7 m in amplitude (Canadian Hydrographic Service 1982) and peak tidal currents of up to 3.0 m s^{-1} being measured near the eastern entrance to the Strait (Osborn et al. 1978). Griffiths et al. (1981) predicted tidally "mixed" areas within Ungava Bay, near Resolution Island and across the mouth of the Strait, which were separated from neighboring stratified waters by tidal fronts. These predictions were based on a numerical model of the M_2 tides from which the stratification parameter, S, was calculated. This parameter is the ratio of the stabilizing effect of surface buoyancy flux due to solar heating to the production of turbulent kinetic energy generated by tidal mixing and is primarily dependent upon $[h/u^3]$ where h is the depth of the water column and u is the tidal velocity averaged over a tidal cycle. The critical values of S for Hudson Strait which mark the transition regions between well-mixed and stratified waters in summer were assumed by Griffiths et al. (1981) to be similar to those found on the shelf seas around the British Isles. However, their analysis neglected freshwater runoff and its stabilizing influence on the buoyancy flux which could change the S values at which transition occurs (see Garrett et al. 1978). Therefore the areal extent of the tidally "mixed" regions predicted by Griffiths et al. (1981) are likely to be modified, especially during July and August with the arrival of the low salinity waters originating from Hudson Bay and Foxe Basin. In spite of these problems, summer infrared (IR) satellite imagery shows the expected cold regions in the general areas designated as "well mixed" (Griffiths et al. 1981) and temperature fronts have been observed by Campbell (1958) at the eastern entrance of the Strait.

Large-amplitude internal waves, observed near the eastern entrance to Hudson Strait (Campbell 1958), may provide additional energy for vertical mixing. However, the extent of the internal wave activity and its importance as a mixing mechanism are unknown.

Vertical mixing through estuarine-type entrainment was suggested by Campbell (1958) as a mixing mechanism in Hudson Strait. He attributed the increase in the near surface salinities from west to east along the southern side of the Strait to mixing associated with the eastward transport of the low salinity waters originating from Hudson Bay and Foxe Basin. However, these same low salinity waters can restrict vertical mixing through increased density stratification. We shall return to the effect of the low salinity water on mixing in Hudson Strait later in the next section.

Biological Implications

We now consider the nutrient enrichment we've proposed for the northern Labrador Shelf and investigate its possible biological consequences. In view of this nutrient flux it is of interest to look at fish catch downstream from Hudson Strait. Figure 4 shows a plot of mean catch of the NAFO subareas 2G–3L (from Cape Chidley to Newfoundland, see also Fig. 1) for the years 1971–77, as well as catch per unit area. It may be seen that in the two northern divisions (2G and 2H)

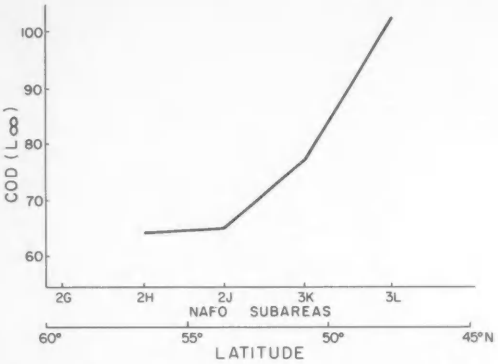

FIG. 5. The length at "largest size" for cod (taken from May et al. 1965) plotted as a function of longitudinal distance along the Labrador–Newfoundland Shelf.

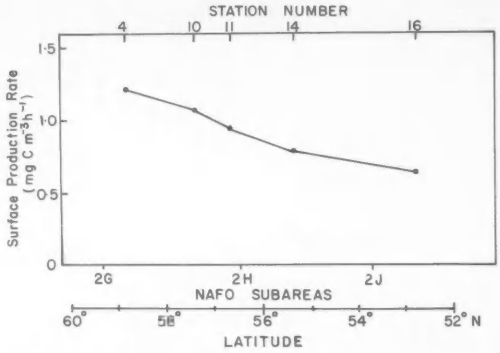

FIG. 6. Surface production rate as a function of longitudinal distance along the Labrador Shelf. Station numbers refer to Irwin et al. (1978).

the catch is very low but increases in a southward direction to a peak in catch per unit area in subareas 2J, 3K approximately 1000 km south of Cape Chidley. This representation is suspect, however, for it may be only a reflection of fishing effort, especially in the northern region with attendant difficulties of ice, inclement weather and low human populations there. For this reason we considered the abundance of seabirds that have been fishing this area for some time. From Brown et al. (1975) we obtained counts of the five most common seabirds feeding on small fish and nesting on the coast — thus requiring for a time, at least, a dependable supply of food. These counts were converted to live weight of birds (R. G. B. Brown, Canadian Wildlife Service, Bedford Institute of Oceanography, personal communication), assigned to the proper division and plotted in Fig. 4. The parallel between birds and fish catch is evident. This is not a reflection of available nesting sites (R. G. B. Brown, personal communication) nor simply a matter of inclement weather or ice conditions, for the nesting birds increase considerably somewhat to the north of division 2G. The bird surveys are recent, thorough, cover several years, and the species are not ship followers for offal. From the bird distributions it appears that at times there is a paucity of suitable food, i.e. small fish on the northern Labrador Shelf.

May et al. (1965) presented comparisons of cod growth for several of the NAFO subareas considered above. The length of cod at "largest size" in the northern areas is found (Fig. 5) to be only a little more than 60% the size of those to the south. Kerr (1979) found that the largest sizes attainable were proportional to the sizes of available prey in a study of lake trout (*Salvelinus namaycush*) and Ogak Lake (Baffin Island) cod, among others. If larger and larger prey sizes were unavailable to the growing fish, maximum size was accordingly restricted (Kerr 1971, 1979). These effects were more important than temperature and density of prey. The southward increase along the Labrador Shelf in the length at "largest size" of cod can therefore be interpreted as due to increasing prey size.

Two apparent conflicting observations have been made of the northern Labrador coast — an adequate nutrient supply but low productivity in terms of large and small fish. Our proposed resolution of this conflict lies in the proximity of the area to an important source of nutrients, Hudson Strait, and the swift currents that prevail there and along the Labrador Shelf. Given a current of about 20 km d^{-1} this allows about a month from Cape Hopes Advance in Hudson Strait (Fig. 1) to the center of subarea 2H for the food chain to develop from nutrients to phytoplankton to zooplankton of a size suitable for small fish (ca. 15 cm) attractive to the birds and food for hungry cod. This is probably not enough time in this subarctic area to proceed from nutrients to phytoplankton to a sizeable population of zooplankton, let alone a population of small fish (G. Riley, Dalhousie University, Halifax, N.S., personal communication) which would be of benefit to the inhabitants of subarea 2H or the nearer 2G. We propose that the additional time (approximately one month) required to reach the southern Labrador Shelf and northern Newfoundland (subareas 2J, 3K; Fig. 1) would allow sufficient time for development of the large zooplankton and small fish. Our hypothesis of the food chain on the Labrador Shelf developing progressively downstream from the primary source of nutrients is similar to the production mechanism proposed by Steven (1975) for the Gulf of St. Lawrence.

The advection southward as the food chain develops suggests a decrease in primary production from north to south along the Labrador Shelf. Surface production data from inshore Labrador Shelf stations (Irwin et al. 1978) show such a decrease (Fig. 6). The slope of the line is statistically different from zero to a level of significance of 0.01 and cannot be explained by temperature or light effects. We recognized that the data are limited in both space and time, and that surface production is not always indicative of integrated production throughout the water column, but it is nevertheless encouraging to note that the only primary production data available for the Labrador Shelf are at least consistent with our hypothesis.

We continue a little further with our considerations that the above chain of events, starting with nutrients in Hudson Strait, culminates in the higher production of fish in subareas 2J and 3K.

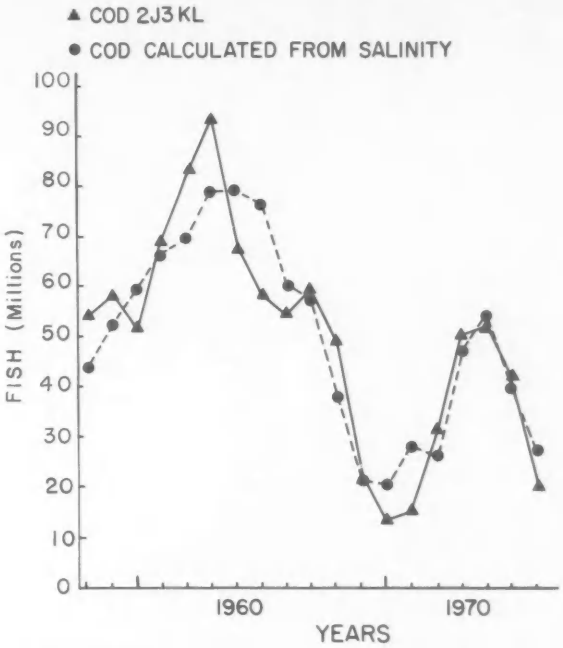

FIG. 7. Atlantic cod (*Gadus morhua*) abundance in NAFO Subareas 2J, 3KL at age 4 from both virtual population analysis and calculated from correlations with Station 27 salinities.

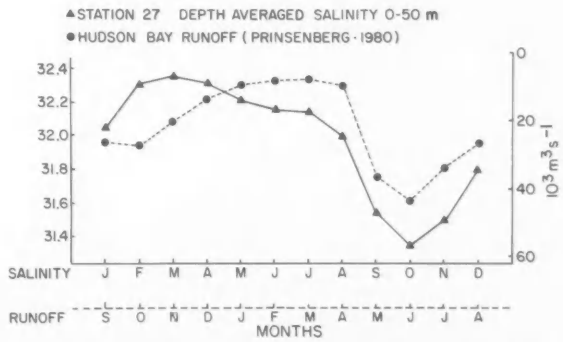

FIG. 8. Seasonality of the depth-averaged (0–50 m) salinity at station 27 off St. John's, Newfoundland and of the freshwater discharge into Hudson Bay.

Labrador and northern Newfoundland cod stocks can be examined in another light. Fluctuations in a nutrient supply as proposed above would be reflected in year to year changes in salinity, inasmuch as the nutrient source is the high salinity water. To examine this expectation a time series for salinity is required. Salinity data have been collected at Station 27 (Fig. 1), 4 km off St. John's, Newfoundland approximately twice monthly since 1954. While further south than desired there are no long-term salinity measurements for the Labrador Shelf. Depth-averaged salinities to 50 m were compared to the best available virtual population estimates of year-class strength of 2J, 3KL cod stock (Wells and Bishop 1980).

The correlation between the age 4 cod for the years 1958–1976 and the corresponding summer salinities for each of the first three years of life of the cod accounted for 80% of the variation ($r = 0.90$, Fig. 7), i.e.

(1) numbers ($\times 10^5$) of cod at age 4

$$= -26360 + 162\,(x_1) + 278\,(x_2) + 406\,(x_3)^2$$

where x_i ($i = 1,2,3$) is the mean depth-averaged salinity at Station 27 for the months July through September in the ith year of the life of the cod. This implies that the year-class strength is determined over the course of the first 3 yr for this cod stock although it also has the effect of smoothing the salinity signal. The positive correlation indicates higher abundance of cod with higher salinity water. The level of significance of the correlation was 0.01 after accounting for the autocorrelation of the time series (see Garrett and Toulany 1981).

The freshwater discharge into Hudson Bay which flows out through Hudson Strait must play an important role. Comparison between the monthly mean freshwater discharge into Hudson Bay (Prinsenberg 1980) and the 0–50 m depth-averaged monthly mean salinities at Station 27 (Fig. 8) shows an inverse relationship when the salinity lags the runoff by 4 mo. This lag corresponds to a velocity of 0.20 m s^{-1} (from northern Hudson Bay to Station 27) and compares with the measured velocities of 0.10–0.40 m s^{-1} along the Labrador Shelf from satellite track drogues (LeBlond et al. 1981), and moored current meters (Lazier 1979). If the relationship between Hudson Bay runoff and salinity at seasonal time scales also applies at longer time scales, the above correlations suggest increased cod catches following years of low runoff. Sufficient Hudson Bay discharge data to test this hypothesis[2] directly are unavailable. However, the St. Lawrence River drainage basin is adjacent to the southern section of the drainage basin of Hudson Bay and the largest amount of runoff into Hudson Bay is from the south (Sanderson and Phillips 1967). Thus an annual signal representative of the St. Lawrence River drainage (RIVSUM, Sutcliffe et al. 1976) was compared with the Labrador cod using 3-yr steps, somewhat as salinity was used above, and a correlation of $r = -0.71$ resulted (with a significance level of 0.05), quite in agreement with the hypothesis. We suggest that the freshwater discharge may act principally as a stratifying influence. With increased discharge the added stratification suppresses mixing within Hudson Strait resulting in less nutrients being made available to the surface layers along the Labrador Shelf. Another interpretation is that in years of high discharge the high nutrient offshore waters are pushed further out of Hudson Strait and hence are less available for mixing. Campbell (1958) found the offshore Atlantic waters penetrated further into the Strait during times of low freshwater discharge (October) than under high discharge conditions (July). Seasonal temperature and salinity data in Hudson Strait are required to determine the actual influence of the fresh water outflow from Hudson Bay.

[2]If these salinities reach 31.16‰ for 3 consecutive years then the number of age 4 cod = 0; an interesting but unlikely result.

Discussion

We have presented evidence to show that nutrients are mixed into the surface layers within Hudson Strait and flow out onto the northern Labrador Shelf. The time required for a food chain to develop, based on these nutrients, together with southward advection by the Labrador Current are proposed as determining the fish distributions along the Labrador Shelf, notably low concentrations to the north and high in the south. Discharge–salinity–cod relationships suggest that in years of high freshwater outflow from Hudson Bay mixing may be suppressed, less nutrients reach the surface layers on the Labrador Shelf and production, from primary to tertiary, decreases. This apparent importance of the freshwater discharge indicates possible effects on the fisheries production along the Labrador Shelf by large hydroelectric development schemes on the watersheds adjacent to Hudson Bay.

Many factors affecting biological production have not been discussed within this paper, notably topographic effects around banks and density fronts, such as that existing off the continental slope of Labrador. The importance of such factors on production for other continental shelves in the Northwest Atlantic is already documented (e.g. Fournier et al. 1977; Cohen et al. 1982). Their relative importance on the Labrador Shelf are, at this time, unknown. Further and more extensive observations are necessary to substantiate (or negate) the food chain hypothesis presented herein.

Acknowledgments

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Responses of Stream Zoobenthos to Enrichment of Gravel Substrates with Cereal Grain and Soybean

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MUNDIE, J. H., S. M. MCKINNELL, AND R. E. TRABER. 1983. Responses of stream zoobenthos to enrichment of gravel substrates with cereal grain and soybean. Can. J. Fish. Aquat. Sci. 40: 1702–1712.

In four separate replicated experiments, cereal grain or soybean was added at a rate of 500 mL/m^2 to standard gravel in parallel troughs in a stream. The invertebrates that colonized the gravel were collected, after 32–65 d, in a net of mesh 350 μm; this retained about 19% of the fauna numerically. Numbers and weights were estimated after instantaneous subdivision, and differences tested by nested ANOVA. The enriched troughs contained 1.5–2.9 times the weight of invertebrates of the controls. Increases in numbers ranged from 1.4 to 1.9 times, and were owing to Chironomidae and Oligochaeta. Ephemeroptera showed a significant increase in only 1 trial. Responses of other groups of insects could not be tested on account of their low abundance. A trial with 1000 mL of grain/m^2 did not produce a proportional increase in fauna. No significant differences were found in the numbers and weights of invertebrates drifting from the control and treatment troughs. We conclude that grain and soybean can be used in the field culture of salmonid food organisms.

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Au cours de 4 expériences reproduites séparément, des grains de céréales ou du soja furent ajoutés au taux de 500 mL/m^2 à du gravier standard dans des auges parallèles placées dans un cours d'eau. Après 32–65 jours, les invertébrés qui avaient colonisé le gravier ont été recueillis à l'aide d'un filet de mailles de 350 μm; ces mailles ont retenu environ 19 % de la faune en nombre. Les nombres et les poids ont été estimés après subdivision instantanée, et les différences déterminées. Les auges enrichies contenaient de 1,5–2,9 fois le poids des invertébrés des témoins. Les augmentations en nombre variaient entre 1,4 et 1,9 fois celles des témoins, les Chironomidae et les Oligochaeta étant responsables de ces augmentations. Les Ephemeroptera ne montrèrent des augmentations significatives que dans 1 essai. À cause de la faible abondance des autres groupes, nous n'avons pu tester leurs réactions. Un essai avec 1 000 mL/m^2 de grain ne donna pas d'augmentation proportionnelle de la faune. On n'a trouvé aucune différence significative de nombres et de poids d'invertébrés dérivant des auges témoins et des auges traitées. Nous concluons que le grain et le soja peuvent être utilisés dans la culture sur le terrain d'organismes pour nourrir les salmonidés.

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MAXIMIZATION of salmonid smolt production from streams of low productivity would seem to depend largely on control of discharge and on increases in production of fish food-organisms (Mundie 1974). The food of salmonids in streams is almost entirely aquatic insects (e.g. Mundie 1969), and the insects themselves live on two main kinds of food: unicellular algae (e.g. diatoms), and detritus colonized by microorganisms (reviewed by Cummins and Klug 1979). This paper therefore addresses the question: what is the response of stream insects, which enter the diet of salmon and trout, to increases in their food materials under conditions of stable discharge?

Since the two common foods of the insects represent the autotrophic and heterotrophic food paths, increases may be effected by inorganic or organic enrichment. The latter was chosen for several reasons: firstly, the cost/benefit ratio of treatments had to be borne in mind if positive results were to have broad application, and apparently suitable inexpensive ingredients, i.e. cereal grains and legumes, are available in abundance. Secondly, complex organic materials would be less likely to become limiting to microbes than would simple inorganic solutions to the growth of algae. Thirdly, previous exploratory work (Mundie et al. 1973) had indicated a pronounced response of some benthic insects to additions of cereal grain to a stream riffle. Finally, there is evidence that wheat grains supply a necessary ingredient for normal development of a caddis fly (Anderson 1977).

We anticipated that the response of insects would have four

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chief aspects: an increase in numbers of individuals over that in the unenriched substrates owing to insects arriving at and remaining and accumulating in the treated sites; increases in numbers owing to reduced mortality; increases in growth rates of individuals; and differences in rates of exodus (behavioral drift) between treated and untreated areas. Since differences in drift might be substantial and could be of consequence to salmonids which feed largely on drifting insects, an attempt was made to estimate them.

Materials and Methods

Field Methods

Grain and soybean were added to gravel (mean size 3 cm, range 1.9–3.9 cm) in 12 parallel wooden troughs placed in riffles in a side-channel of the Big Qualicum River, Vancouver Island, B.C. Details of the channel, which has controlled discharge, are given in Mundie and Mounce (1978). Each trough was 2.43 m long, 21.5 cm wide (area 0.52 m^2), and 40.6 cm high, and the depth of gravel in each was 8.8 cm. Depth of water over the gravel was 4 cm, and identical discharges of 1 L/min were maintained by partially occluding the upstream inlets of each trough with a wooden partition which left a vertical slot through which the water passed.

We allowed 3 wk (Williams et al. 1977) for the gravel to be colonized by drifting invertebrates. Grain or soybean was then soaked in hot water for a few minutes to prevent germination and was evenly distributed in the treatment troughs where it settled in the interstices of the gravel. Treatment troughs alternated with the control ones, the arrangement of the 12 parallel troughs giving replication of controls and treatment.

Four experiments were carried out over 2 yr as follows:

Expt.	Duration	Mean temp. °C	Treatment	Replication (No. of troughs)
1	Mar. 25 to May 14	9.5	—	Controls 6
			Soybean 250 mL	Treatment 6
2	Mar. 25 to May 21	10.4	—	Controls 5
			Wheat 250 mL	Treatment 5
3	Aug. 22 to Sept. 22	12.5	—	Controls 3
			Wheat 250 mL	Treatment 2
			Wheat 500 mL	Treatment 2
4	June 2 to Aug. 6	11.5	—	Controls 3
			Wheat 250 mL	Treatment 3
	Overnight drift was collected on 10 occasions between June 29 and July 29	11.5	—	Controls 6
			Wheat 250 mL	Treatment 6

After 4–9 wk, depending on water temperature which influenced the rate of decomposition of the grain, the benthos and detritus were collected from each trough. The grain was examined prior to sampling. If the individual grains were hard, insufficient time had been allowed for breakdown and consumption; if only the husks were left, for the most part, then the period had been too long. The time was taken to be right when the contents of the grain were milky. A net, supported by a rigid frame, was inserted into slots at the outlet, the restricting partition at the entrance of the trough was removed to increase the water velocity and so facilitate transport of materials, and the gravel was agitated and turned over with a small garden fork. The downstream half of a trough was worked over first, then the upstream, and finally the whole length was done again. The net was removed and replaced promptly with a clean one 3 times during this process to prevent clogging and back-washing. Collecting lasted about 20 min per trough.

The net had a 350 μm mesh. This was considered adequate for estimating invertebrates likely to enter the diet of salmonids, and its use avoided the clogging difficulties of finer nets. A sample, however, was taken on one occasion with a 50 μm net to obtain a measure of the proportion of animals lost through the coarser mesh. Only the downstream half of the trough was disturbed; even so, the net had to be washed and replaced repeatedly. A sample from a trough enriched with 250 mL of grain and collected with the 350 μm net typically had a settled volume of about 1200 mL.

Logs were placed across the channel downstream of the troughs to provide a shallow weir over which the water discharged. This drop was used to collect drifting invertebrates in plastic buckets with screen bottoms and side ports (Fig. 1). The drift passed from the troughs along rigid plastic pipes (int diam 38 mm) which collected aliquot samples of water. The upstream ends of the pipes, which were cut obliquely and broke the water surface, just entered the troughs. The assembly of pipes was lifted above the water during daylight hours and lowered into place for overnight sampling. Samples were collected each morning.

Laboratory Methods

Estimation of numbers and weights of the benthos collected in the net was by subdivision into very many (82) units in which the numbers of animals were believed to be distributed randomly (Mundie 1971a; Williams 1981). A few of these (10) were then randomly selected for counting and weighing.

Before dividing the total preserved sample we poured it onto an 8 mm sieve to retain leaves and coarse debris which were thoroughly washed. Dislodged invertebrates were returned to the bulk of the sample, except for rare exceptionally large animals; these were discarded as they could greatly influence weights. The sample was then poured into a plastic washbowl (36 cm by 30 cm, 12 cm deep) with sufficient water to ensure a loose suspension of the material. The bowl was then emptied with a circular motion into a plastic bucket which was about half full of water and had the bottom covered with 82 upright glass tubes each 95 mm by 23 mm. The tubes covered 69.40% of the floor of the bucket, and 1 represented 0.846% of the floor area. The material was settled for 12 h. Some water was then siphoned off without disturbance and 10 tubes were selected at random. Counts were made under a microscope capable of 50× magnification. Grains were dissected for larvae. Weights of insects were obtained after drying the counted animals for 12 h at 110°C. Data were treated by nested analysis of variance.

The counts in the tubes from collections with the 350 μm net ranged typically, in the controls, from 80 to 250 animals

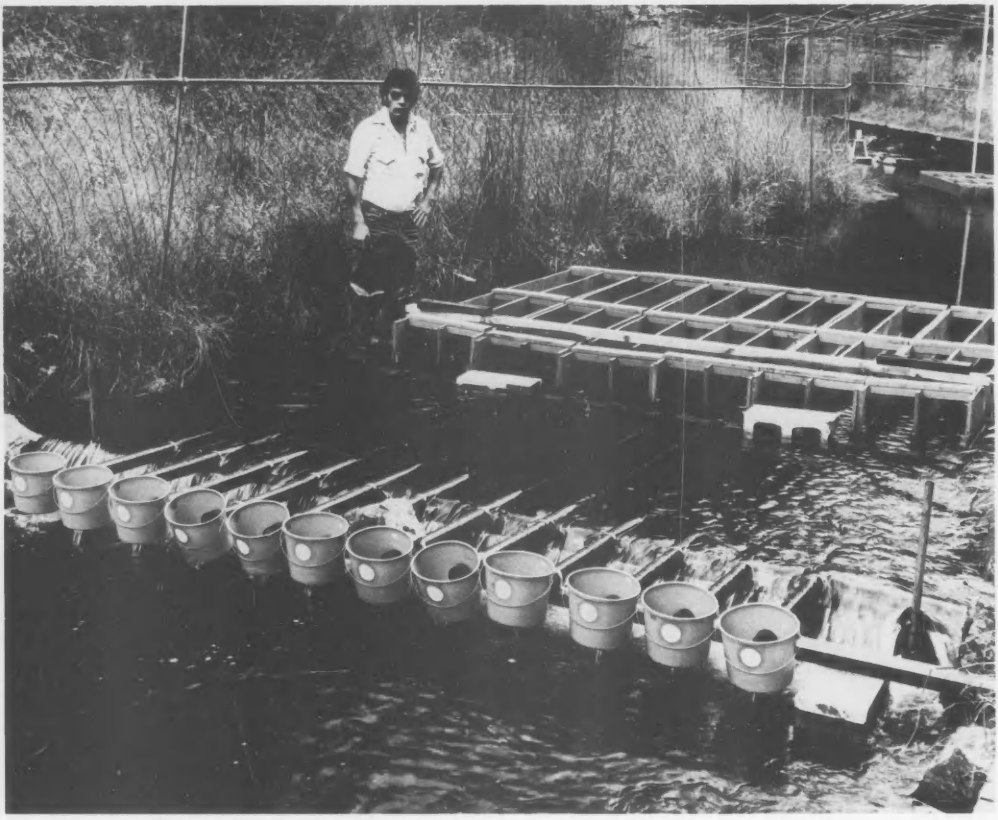

FIG. 1. The experimental troughs and weir for collecting invertebrates.

per tube and in the treatments from 170 to 450 animals per tube. Contrary to expectations, the invertebrates did not settle into the tubes randomly. Random counts would give a Poisson distribution and the mean of the counts would equal the variance. The variance of the counts, however, was about 10 times the mean. For example, the variance was 2000 for a mean of 200 and 4500 for a mean of 350. Variances were positively correlated with means for both numbers and weights. This discrepancy with earlier results is attributed to the larger counts per tube; formerly, counts per tube tended to range between 30 and 100 animals (Mundie 1971). With higher density clumping occurs.

The counts and weights were therefore transformed by $\log_e (x + 1)$ making the variance independent of the mean. Separate nested ANOVAs were carried out on the following data: total weights, total numbers, and individually on the numbers of Chironomidae, Ephemeroptera, Trichoptera, Plecoptera, Simuliidae, Oligochaeta, terrestrial taxa, and "others." The last group comprised uncommon invertebrates (flatworms, leeches, and *Hydra*). The tests were carried out using software from the International Mathematical and Statistical Library. The sources of variation tested were: between troughs within treatments and controls, and between treatment and control troughs.

The samples of drift were not subdivided; each was counted and weighed in entirety. Large insects were not found in the drift.

Results

The invertebrates encountered were those of a clean soft water gravel-bed stream (Table 1). Single collections with a 350 and 50 μm net were taken in November (13°C) to obtain an approximate measure of loss of animals through the coarser net (Table 2). The 350 μm net was used to sample one control trough, and the 50 μm net was used to sample another, but only the downstream half of the trough was disturbed for the 50 μm sample. On a unit area basis the coarser net collected 19% as much as the fine, the difference being due mainly to lost chironomids. In 1 tube from the 50 μm collection, 80% of the insects had headwidths of 100 μm or less (Fig. 2). Substantial loss through the 350 μm net is therefore explic-

TABLE 1. Genera of commoner invertebrates collected in all experiments.

Ephemeroptera	Plecoptera	Trichoptera
Baetis	*Alloperla*	*Hydropsyche*
Ephemerella	*Isoperla*	*Rhyacophila*
Ameletus	*Nemoura*	*Glossosoma*
Paraleptophlebia		
Rithrogena	Oligochaeta	
Cinygma	*Nais*	
Heptagenia	*Dero*	
	Chaetogaster	
Diptera		
Chironomidae	Simuliidae	Tipulidae
Ablabesmyia	*Simulium*	*Antocha*
Corynoneura	*Prosimulium*	
Thienemanniella		
Eukiefferiella		
Brillia		
Psectrocladius		
Cricotopus		
Polypedilum		
Phaenopsectra		
Microtendipes		
Rheotanytarsus		
Micropsectra		

able (cf. Mundie 1971; Hummon 1981). The loss, however, will vary seasonally and with the quantity of silt present, as some larvae which are capable of passing through the coarse net will be retained in the presence of much silt.

Chironomids, Ephemeroptera, and oligochaetes made up most of the numbers (Table 3). The different proportions of midges and mayflies in the controls of the four experiments can be ascribed to net selection acting on seasonally different size-distributions. In treatments these proportions could be influenced, of course, by the enrichment.

A 2-fold increase in weight of benthos occurred in the troughs treated with soybean (Table 4). Numbers increased 1.48-fold and this was owing to chironomids and oligochaetes. There was no response from mayflies. The other categories of invertebrates occurred in numbers too low for the tests of significance to be valid. In this experiment, and in others, significant differences were found among control troughs and among treatment troughs. Treatment effects, however, exceeded these.

Experiment 2 (Table 5) gave a 1.5-fold increase in weight of invertebrates with wheat treatment and nearly a 1.9-fold increase in numbers. The increases were again owing to chironomids and oligochaetes, although there was a significant increase in mayflies ($P < 0.05$).

Experiment 3 (Table 6) showed a 1.7-fold increase in weight of benthos with the addition of 250 mL of grain, and a doubling with 500 mL. The null hypothesis of no difference in mean biomass was rejected at a probability of 0.01. Despite the fact that the ANOVA produced a highly significant result, a Newman–Keuls multiple range test was not powerful enough to discern which means were different. It is clear that the doubling of biomass at the 500 mL level is significant. It is not possible, however, to claim that the 1.7-fold increase at the 250 mL level of grain application is significant. This

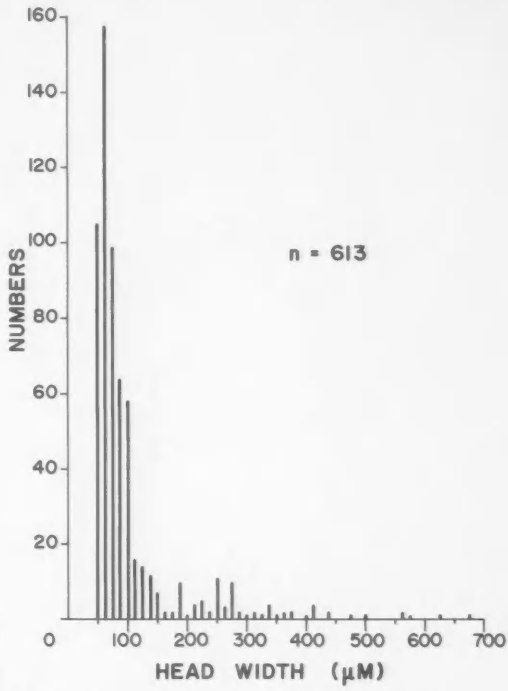

FIG. 2. Size distribution of head widths of insects sampled with a 50 μm net; 613 insects settled into 1 tube.

TABLE 2. Collections from control troughs. One trough sampled with a 350 μm net; half a trough sampled with a 50 μm net; n = number of tubes examined.

	350 μm net (entire trough)	50 μm net (0.5 trough)
n	3	3
no. of animals per tube, $\bar{x} \pm$ SE	288 ± 26.0	761 ± 42.4
	Composition (%)	
Chironomidae	54	79
Ephemeroptera	26	11
Plecoptera	2	1
Trichoptera	3	1
Tipulidae	<1	1
Simuliidae	<1	<1
Oligochaeta	10	7
Turbellaria	1	2

should not imply that a real effect owing to treatment at the 250 mL level is missing. We believe that the 1.7-fold increase in biomass is real and is consistent with the other three experiments. A doubling of the amount of grain did not produce a proportionate increase in weight and numbers of invertebrates. The numerical increases in this experiment were again attributable to chironomids and oligochaetes.

TABLE 3. Percent composition of the commoner taxa in controls (C) and treatments (T), and ratio of total numbers (n) in C and T.

Taxa	Expt. 1		Expt. 2		Expt. 3			Expt. 4	
	C	T	C	T	C	T low	T high	C	T
Chironomidae	70	75	57	58	45	57	61	82	82
Ephemeroptera	19	14	31	23	42	24	24	11	8
Plecoptera	1	1	2	1	3	2	1	2	1
Trichoptera	1	1	2	1	2	1	1	1	1
Simuliidae	4	2	1	1	1	1	1	1	1
Oligochaeta	5	7	5	14	4	12	10	4	7
Others	1	1	1	1	3	1	1	1	1
n for C	11618		5293		8569			6287	
n for T		17370		9720		14207	14731		10391
n_C/n_T	1/1.49		1/1.83			1/1.66	1/1.71	1/1.65	

TABLE 4. Experiment 1, Soybean, 50 d at 9.5°C; 6 control troughs, 6 treatment troughs. $*P < 0.05$; $**P < 0.01$.

Source of variation	DF	SS	MS	F	SS	MS	F
	Total wt (mg)				Total nos		
Total	119	22.348			12.834		
Treatment	1	11.682	11.682	64.69**	4.785	4.785	15.11**
Troughs	10	1.806	0.181	2.20*	3.166	0.317	7.00**
Error	108	8.860	0.082		4.884	0.045	
Treatment	$\bar{x}$ 39.20, SD 11.97				$\bar{x}$ 289.63, SD 73.51		
Control	$\bar{x}$ 20.84, SD 7.16				$\bar{x}$ 194.51, SD 50.49		
	Chironomidae nos				Ephemeroptera nos		
Total	119	16.761			9.844		
Treatment	1	6.983	6.983	15.70**	0.252	0.252	0.95
Troughs	10	4.448	0.445	9.01*	2.650	0.265	4.12
Error	108	5.329	0.049		6.942	0.064	
Treatment	$\bar{x}$ 216.83, SD 54.90				$\bar{x}$ 40.13, SD 13.04		
Control	$\bar{x}$ 135.40, SD 41.42				$\bar{x}$ 36.15, SD 10.43		
	Plecoptera nos				Trichoptera nos		
Total	119	43.482			36.288		
Treatment	1	0.082	0.082	0.03	0.449	0.449	0.52
Troughs	10	25.840	2.584	15.89**	8.664	0.866	3.44**
Error	108	17.560	0.163		27.175	0.252	
Treatment	$\bar{x}$ 0.88, SD 1.53				$\bar{x}$ 3.383, SD 1.96		
Control	$\bar{x}$ 0.78, SD 1.52				$\bar{x}$ 2.867, SD 1.84		
	Simuliidae nos				Oligochaeta nos		
Total	119	29.574			39.049		
Treatment	1	2.030	2.030	1.57	15.290	15.290	17.23**
Troughs	10	12.931	1.293	9.56**	8.876	0.888	6.44**
Error	108	14.613	0.135		14.883	0.138	
Treatment	$\bar{x}$ 5.30, SD 3.69				$\bar{x}$ 21.20, SD 9.37		
Control	$\bar{x}$ 6.81, SD 3.23				$\bar{x}$ 9.90, SD 4.65		
	Terrestrial items nos				Others nos		
Total	119	35.112			35.849		
Treatment	1	0.081	0.081	0.16	4.005	4.005	9.05*
Troughs	10	4.911	0.491	1.76	4.427	0.443	1.74
Error	108	30.120	0.279		27.417	0.254	
Treatment	$\bar{x}$ 1.30, SD 1.24				$\bar{x}$ 0.60, SD 0.76		
Control	$\bar{x}$ 1.15, SD 1.17				$\bar{x}$ 1.46, SD 1.42		

TABLE 5. Experiment 2, wheat, 57 d at 10.4°C; 5 control troughs, 5 treatment troughs. $*P < 0.05$; $**P < 0.01$.

Source of variation	DF	SS	MS	F	SS	MS	F
	Total wt (mg)				Total nos		
Total	99	26.281			16.250		
Treatment	1	4.580	4.580	16.81**	10.499	10.499	105.28**
Troughs	8	2.179	0.272	1.26	0.798	0.100	1.81
Error	90	19.522	0.217		4.953	0.055	
Treatment	$\bar{x}$ 31.56, SD 14.57				$\bar{x}$ 197.24, SD 41.98		
Control	$\bar{x}$ 20.37, SD 9.08				$\bar{x}$ 103.54, SD 26.75		
	Chironomidae nos				Ephemeroptera nos		
Total	99	22.060			13.700		
Treatment	1	14.146	14.146	40.90**	1.291	1.291	6.59*
Troughs	8	2.767	0.346	6.05**	1.568	0.196	1.63
Error	90	5.147	0.057		10.841	0.120	
Treatment	$\bar{x}$ 113.34, SD 24.64				$\bar{x}$ 45.38, SD 16.09		
Control	$\bar{x}$ 54.44, SD 18.20				$\bar{x}$ 35.96, SD 12.78		
	Oligochaeta nos						
Total	99	128.281					
Treatment	1	93.180	93.180	50.51**			
Troughs	8	14.757	1.845	8.16**			
Error	90	20.345	0.226				
Treatment	$\bar{x}$ 28.44, SD 10.11						
Control	$\bar{x}$ 4.20, SD 3.74						

TABLE 6. Experiment 3, wheat at 2 levels; 32 d at 12.5°C; 3 control troughs, 2 low level treatment and 2 high level treatment troughs. $*P < 0.05$; $**P < 0.01$.

Source of variation	DF	SS	MS	F	SS	MS	F
	Total wt (mg)				Total nos		
Total	69	16.160			6.203		
Treatment	2	6.752	3.376	39.459**	3.579	1.790	29.615**
Troughs	4	0.342	0.086	0.595	0.242	0.060	1.598
Error	63	9.065	0.144		2.382	0.038	
Low treatment	$\bar{x}$ 28.62, SD 12.68				$\bar{x}$ 348.30, SD 72.87		
High treatment	$\bar{x}$ 35.70, SD 11.86				$\bar{x}$ 323.80, SD 66.08		
Control	$\bar{x}$ 17.40, SD 9.84				$\bar{x}$ 212.50, SD 44.41		
	Chironomidae nos				Ephemeroptera nos		
Total	69	11.342			6.177		
Treatment	2	8.794	4.397	39.726**	1.360	0.680	4.471
Troughs	4	0.443	0.111	3.311*	0.608	0.152	2.278
Error	63	2.106	0.033		4.208	0.067	
Low treatment	$\bar{x}$ 198.80, SD 37.20				$\bar{x}$ 82.70, SD 26.55		
High treatment	$\bar{x}$ 208.30, SD 43.49				$\bar{x}$ 61.70, SD 16.63		
Control	$\bar{x}$ 99.20, SD 20.70				$\bar{x}$ 84.80, SD 22.24		
	Oligochaeta nos						
Total	69	53.244					
Treatment	2	36.918	18.459	10.932*			
Troughs	4	6.754	1.689	11.113**			
Error	63	9.572	0.152				
Low treatment	$\bar{x}$ 49.95, SD 24.81						
High treatment	$\bar{x}$ 39.05, SD 20.11						
Control	$\bar{x}$ 9.20, SD 4.09						

TABLE 7. Experiment 4, wheat, 65 d at 11.5°C; 3 control troughs, 3 treatment troughs. *$P < 0.05$; **$P < 0.01$.

Source of variation	DF	SS	MS	F	SS	MS	F
	Total wt (mg)				Total nos		
Total	59	24.887			6.782		
Treatment	1	17.211	17.211	23.09**	3.992	3.922	21.72**
Troughs	4	2.981	0.745	8.57**	0.722	0.181	4.56**
Error	54	4.695	0.087		2.138	0.040	
Treatment	$\bar{x}$ 41.48, SD 13.41				$\bar{x}$ 348.56, SD 62.60		
Control	$\bar{x}$ 14.18, SD 5.85				$\bar{x}$ 211.86, SD 54.97		
	Chironomidae nos				Ephemeroptera nos		
Total	59	7.556			5.460		
Treatment	1	4.203	4.203	12.88*	0.417	0.417	2.17
Troughs	4	1.305	0.326	8.60**	0.770	0.192	2.43
Error	54	2.048	0.038		4.274	0.079	
Treatment	$\bar{x}$ 286.56, SD 52.81				$\bar{x}$ 28.66, SD 8.04		
Control	$\bar{x}$ 172.13, SD 48.60				$\bar{x}$ 24.36, SD 7.70		
	Oligochaeta nos						
Total	59	28.956					
Treatment	1	17.359	17.359	46.90**			
Troughs	4	1.480	0.370	1.98			
Error	54	10.117	0.187				
Treatment	$\bar{x}$ 24.03, SD 9.90						
Control	$\bar{x}$ 7.70, SD 3.59						

Experiment 4 (Table 7) produced the greatest increase in weight (2.9-fold) accompanied by a 1.6-fold increase in numbers. The midges and worms were again responsible.

The nested ANOVA was repeated for Experiment 1 without transforming the data. The results were the same. This is attributed to the high counts and to the likelihood of the means of counts being normally distributed. A *t*-test on total numbers in treatment and control in Experiment 1, and a Mann–Whitney test also gave the same level of significance.

Ten samples of overnight drift were taken between June 29 and July 29. Each comprised collections from 6 control and 6 treatment troughs (Fig. 1). The very abundant nymphal exuviae were not counted. The remaining drift consisted in total of 7876 chironomid pupal exuviae and 6308 invertebrates. The commonest insects were chironomids; about 60% of these were Orthocladiinae and 30% Tanytarsini. Chironomini and Tanypodinae were uncommon. We found (Table 8) that no significant differences in numbers of invertebrates leaving the control and treatment troughs were detectable on the 10 occasions of sampling. The weights gave an identical result; for these, none of the calculated F statistics was significant at a probability of 0.05. It was concluded that the enrichment did not increase drift, unless any increases that did occur were masked by the numbers of invertebrates flowing through the troughs from upstream of them.

Discussion

METHODS

Any attempt to measure the response of stream benthos to a treatment raises the familiar intractable problems of estimating benthos precisely. We used troughs with *standardized* gravel to avoid sampling natural substrates and to reduce heterogeneity; the entire contents of the troughs were collected and subsampled. Yet drifting invertebrates could immigrate into and emigrate from the sampled areas, so the method was appropriate in terms of the four aspects of response identified in the introduction. Results may therefore be used to judge whether a larger-scale treatment of a stretch of stream is warranted.

Gravel of a limited size-range, however, initially free of sand and silt, favors invertebrate production. Colonization is maximal in the 2.5–3.5 cm range, the reason being that this size provides more living space and collects detritus — a food of the insects — more effectively than a natural mixture of sizes (Rabeni and Minshall 1977). High quantities of detritus can override any selective effects of physical heterogeneity of substrate (Williams 1980). The biomass of invertebrates in selected gravel may therefore be 6 times that of a natural riffle (Shaw and Minshall 1980) although precise comparison is elusive because of unavoidable differences in the techniques of sampling the two habitats. (Comparison of estimates of the trough fauna with that of a gravel stretch of the Big Qualicum River could be only approximate.). Furthermore, the percentage composition of the species in selected gravel and in natural riffles varies substantially (Shaw and Minshall 1980).

A natural stream fauna should therefore be lower in numbers and biomass per unit area than the fauna of the troughs, but it is difficult to say whether its response to a single treatment, using the quantities employed in this study, would be

TABLE 8. ANOVA in number of drifting invertebrates on 10 occasions; 6 control troughs, 6 treatment troughs.

Date	Source of variation	DF	SS	MS	F	Date	SS	MS	F
June 29	Between groups	1	0.0741	0.0741	0.97	July 9	0.1221	0.1221	2.31
	Within groups	10	0.7646	0.0765			0.5291	0.0529	
	Total	11	0.8387				0.6512		
	Treatment $\bar{x}$ 86.00, SD 30.39						$\bar{x}$ 117.50, SD 18.86		
	Control $\bar{x}$ 96.83, SD 15.91						$\bar{x}$ 147.00, SD 39.46		
July 3	Between groups	1	0.0476	0.0476	1.14	July 13	0.0558	0.0558	0.42
	Within groups	10	0.4177	0.0418			1.3228	0.1323	
	Total	11	0.4653				1.3786		
	Treatment $\bar{x}$ 84.83, SD 21.46						$\bar{x}$ 121.67, SD 52.47		
	Control $\bar{x}$ 94.33, SD 12.09						$\bar{x}$ 128.83, SD 20.54		
July 6	Between groups	1	0.0121	0.0121	0.17	July 15	0.0286	0.0286	0.33
	Within groups	10	0.6972	0.0697			0.8685	0.0868	
	Total	11	0.7093				0.8971		
	Treatment $\bar{x}$ 119.00, SD 32.68						$\bar{x}$ 120.83, SD 39.98		
	Control $\bar{x}$ 111.33, SD 25.97						$\bar{x}$ 132.67, SD 39.33		
July 20	Between groups	1	0.1695	0.1695	2.90	July 28	0.3583	0.3583	4.11
	Within groups	10	0.5843	0.0584			0.8727	0.0873	
	Total	11	0.7538				1.2310		
	Treatment $\bar{x}$ 96.83, SD 26.07						$\bar{x}$ 88.50, SD 12.29		
	Control $\bar{x}$ 122.17, SD 28.67						$\bar{x}$ 133.17, SD 55.88		
July 22	Between groups	1	0.2197	0.2197	4.18	July 29	0.0003	0.0003	0.01
	Within groups	10	0.5258	0.0526			0.5939	0.0594	
	Total	11	0.7454				0.5943		
	Treatment $\bar{x}$ 144.00, SD 35.60						$\bar{x}$ 128.00, SD 27.63		
	Control $\bar{x}$ 108.33, SD 20.60						$\bar{x}$ 127.83, SD 32.56		

more or less than 2 fold. What is clear is that maximization of benthic production would be attainable with a combination of gravel of selected size and enrichment.

We suspect that error in the trough method arose from differences in thoroughness of disturbance of the gravel and washing the nets. Although the procedure is standardized (two people working for a set time on each trough in sequence) differences can occur. It would be desirable to have a method that did not employ a net or sieves. This would necessitate taking much smaller samples and settling without sieving, so that counts of all sizes of animals were obtained. This would be practical for most of the invertebrates but not for the relatively uncommon largest members; these of course greatly affect weights. It might be necessary to have a different procedure for dealing with them. (The difference between the smallest common insects in stream benthos, i.e. first instars of chironomids, and the largest, e.g. final instar Plecoptera nymphs, can be more than 20 fold in length and 100 fold in weight. It seems unreasonable to expect a single sampling technique to be adequate for both sizes. No one would attempt to sample mammals of this difference in size with one technique.) There is need for work, therefore, on the possibilities of using unsieved material (cf. Hummon 1981).

Although the counts in the tubes were found not to be randomly distributed this does not nullify the method. It would be desirable to obtain a Poisson distribution of settled invertebrates to reduce the amount of counting, and this might be done by diluting the samples and by using a larger container with many more tubes, but the present method has merit as it is simple and can deal with samples of any density. The procedure has the advantage that the sample is instantaneously and completely divided into all possible subsamples. The subdivision is not affected by the specific gravity of the organisms (e.g. the occurrence of cases and shells). Any bias in the distribution of settled animals is eliminated by selecting the tubes at random. (This could be formalized by covering the tubes with a numbered lattice, and then selecting them by means of a table of random numbers.) Moreover, there is flexibility in the numbers of tubes that can be examined, for additional tubes may be drawn to improve estimates of uncommon animals without further subsampling (cf. Cassie 1971, p. 188–189).

RESPONSE

We probably underestimated the effects of enrichment because our measurements excluded both very small abundant, and very large rare, invertebrates, although the activities of these animals were included in the experiments. The enriched troughs contained 1.4–1.9 times the numbers, and 1.5–2.9 times the weight of invertebrates of the control troughs, and these differences were due to Chironomidae and Oligochaeta. There was no evidence from our analysis that other invertebrates increased in weight but not numbers.

A doubling of the amount of grain did not produce a proportionate increase in weight and numbers of invertebrates. This is presumably because the decaying material was abundant enough to reduce the interstitial flows through the gravel, and perhaps also oxygen.

Somewhat unexpectedly there was no response (with one exception) from mayflies. The other categories of invertebrates occurred in counts that were too low for the tests of significance to be applied. Yet some of these might be expected to respond, e.g. carnivorous Plecoptera living off chironomids.

It is not possible to say whether soybean was better than grain at producing a response. Availability and local cost of materials are likely to determine what is chosen. Nor can an optimum duration of treatment be stated. Apart from water temperature the seasonal cycle of common organisms will influence this.

Beijerinck's famous interpretation, that everything is everywhere and the milieu selects, is the assumed explanation of the colonization of the troughs and the increases in the treatments. The higher numbers and weights are attributed to the organics serving as food in some form, although it could be argued that the organics serve only as an attractive substrate in which invertebrates shelter. Growth rates of individual organisms in controls and treatments were not examined (differences in mean size were not apparent by inspection) but even differences in sizes could be attributed to selective colonization and not to faster growth. Nevertheless it seems reasonable to assume that the increases in chironomids and oligochaetes are a response to food supplied by decomposing organic material.

Recent community studies substantiate the fact that most benthic species ingest a component of detritus, i.e. dead organic material with its associated micro-flora (Anderson and Sedell 1979). The main source of detritus in streams is fragmented decaying leaves, and both the leaves themselves and their associated micro-flora serve as food (cf. Marcus and Willoughby 1978). The food quality of detritus, as measured by protein content, affects growth rates of insects (Shepard and Minshall 1981), and it has been demonstrated for one chironomid (*Paratendipes albimanus*) that growth rate is linearly related to microbial biomass as measured by ATP content or heterotrophic respiration (Ward and Cummins 1979). Furthermore this species can produce multiple generations if continuous supplies of high quality food are available to it (Ward and Cummins 1979).

Invertebrate assimilation efficiencies are higher for ingested microorganisms than for fragmented vascular tissue, but the microbial biomass associated with detritus is low (Cummins and Klug 1979). A substrate that promotes microorganisms would therefore be nutritionally valuable. Clear evidence of this is provided by enrichment of an artificial stream with sucrose (Warren et al. 1964). This resulted in extensive growth of the bacterium *Sphaerotilus*. Apparently all taxonomic groups of insects increased in biomass in response to this, with chironomids showing the greatest increase (about 27 fold in standing stock).

It is not possible to say whether the invertebrates in the troughs derived food mainly from the microbes and fungi (the latter were conspicuous) associated with decomposition, or from the grains themselves. Grain, of course, is a common food of many groups of terrestrial insects and it is employed extensively in the preparation of diets for mass rearing of insects, diets containing wheatgerm being particularly successful (Vanderzant 1974). Soybeans are also used, although they contain toxic factors that have to be destroyed by heat treatment.

These materials, however, are dry, and great efforts are made to maintain their nutritional quality during storage, otherwise enzyme reactions destroy the nutrients and form toxic products. The nutritional value of decomposing grain and soybean for insects cannot readily be compared, therefore, to that of the dry product.

Although detritus may be the main food of the smaller instars of stream insects, rates of development and growth may be largely dependent on an animal diet. For example, the tanypodine *Ablabesmyia monilis* develops poorly on detritus but well on a diet containing *Stentor* and oligochaetes (Mackey 1977). Again, the trichopteran *Hydropsyche* shows larval increases in weight 7.0 times greater on a diet of enchytraeids, and 4.6 times greater on diatoms, than on leaf detritus (Fuller and Mackay 1981). It is noteworthy, therefore, that the decomposing grain and soybean support oligochaetes and chironomids because they in turn enter the diet of chironomids (Loden 1974) and carnivorous insects (Warren et al. 1964).

Organic fertilizers are used extensively in pond aquaculture (Bardach 1978) and their use is growing because of rising costs of inorganic fertilizers. The pathways by which they promote invertebrates for fish-food are poorly understood, but unicellular algae comprise an important one. For example the mass culture of *Chironomus tentans* is possible in ponds fertilized with soybean meal (Sadler 1935); here the insect lives omnivorously. It is difficult, however, to relate this lentic process to decomposition of legumes and grain in the gravel substrate of streams.

Many food substances have been tested as diets for chironomids and other freshwater invertebrates. Commercial dog biscuits (Biever 1971), powdered liver, yeast (Konstantinov 1952) and commercial fish food (Yashouv 1970; Williams et al. 1977; Rach 1982) are acceptable, but their application to streams would be impracticable on grounds of cost or pollution.

Drift

Currently there are two main hypotheses to account for drifting invertebrates in streams. The most widely favored is that drift is linearly related to the density of benthic invertebrates, i.e. drift is caused by a random movement of invertebrates off the substratum and is proportional to benthic abundance. The second is that drift occurs when the carrying capacity of the substrate for zoobenthos is exceeded. This capacity is a function of available food, and the amount of drift is a measure of the extent to which it is exceeded (Hildebrand 1974).

The drift collections showed no increase in invertebrates drifting from the treatment troughs. This result therefore supports the second hypothesis. Two investigations can be similarly interpreted. Warren et al. (1964) found that the *total* drift

in enriched sections of an artificial channel was much less than, and differed in composition from, that in the unenriched sections. (Chironomids were conspicuous drifters in the enriched section where they were produced in very great abundance in *Sphaerotilus*.) The explanation proposed is that reduced competition for food in the enriched sections resulted in reduced drift. Again, Hughes (1970) found that he could depress both upstream and downstream movements of *Gammarus pulex* in an artificial stream by providing them with food.

If drift is not increased by enrichment it follows that the benefits of enrichment to salmonids must accrue from their feeding on the benthos (a characteristic of trout species) and on emerging insects. Pupae and emerging adult chironomids are highly available to coho (Mundie 1971b) and chinook salmon (*O. tshawytscha*) (U. Orr, Fisheries and Oceans, Prince Rupert, B.C., unpublished data).

Although the above may explain the results obtained, it could be argued that there might have been an increase in the drift from the treatment troughs, but this was not detected as it was masked by much larger quantities of drift passing through all the troughs from upstream. Only further work could settle this point.

Future Work

The treatment in troughs over 4 weeks gave a measurement of the benthic response; it did not give a measure of increased food available to fish. To get this, enrichment on a larger scale is required, and emphasis could be placed on assessing emergence. This is a more tractable problem than assessment of changes in benthos. Increases in available food following repeated (say monthly) additions of organics from spring to fall should be estimated and a cost : benefit analysis attempted.

Stream enrichment is in its infancy, and it is probably desirable, if different materials are to be tried, that both small-scale trough experiments and large-scale treatments of stretches of stream be undertaken. In this way the case for stream enrichment can be built up. Finally, the additional advantages — and perhaps the ones that will make the cost/benefit ratio acceptable — of stable discharge and selected gravel should be borne in mind. These are most readily attainable in side-channels of streams (Mundie 1974).

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Trophic State Classification of Lakes with Aquatic Macrophytes[1]

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We developed an approach for assessing the trophic status of lakes having growths of aquatic macrophytes because conventional criteria for classifying trophic state emphasize conditions in the open water and ignore the nutrients, plant biomass, and production associated with macrophytes. We propose that a potential water column nutrient concentration be determined through adding the nutrients contained in macrophytes to those in the water. Potential nutrient concentrations can be used in existing indices to classify lake trophic status. This approach permits a first approximation of the potential impact of macrophytes on lake trophic state.

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Parce que les critères conventionnels de classification de l'état trophique des lacs mettent l'accent sur les conditions existant en eau libre et ignorent les substances nutritives, la biomasse végétale et la production associée aux macrophytes, nous avons mis au point une approche de l'évaluation de l'état trophique de lacs riches en macrophytes aquatiques. Nous proposons qu'on détermine une concentration potentielle de nutriments dans la colonne d'eau en ajoutant ceux contenus dans les macrophytes à ceux présents dans l'eau. Les concentrations potentielles de substances nutritives peuvent être utilisées dans les indices actuels pour classifier l'état trophique d'un lac. Avec cette approche, on peut faire une première approximation de l'impact possible des macrophytes sur l'état trophique d'un lac.

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OUR purpose in this paper is to present an approach for assessing the trophic status of lakes having growths of aquatic macrophytes. An objective trophic state classification system for lakes has long been sought by limnologists to rank and compare lakes with different structural and functional characteristics (Naumann 1919, 1932; Thienemann 1921; Birge and Juday 1927). In recent years, several trophic classification systems have been developed to characterize lakes and to predict their future conditions given various anthropogenic activities (Likens 1975; Carlson 1977, 1979; Walker 1979; Forsberg and Ryding 1980). Although these systems have several advantages including minimal data requirements, sensitivity in ranking trophic status, and ease of interpretation, they give no consideration to aquatic macrophytes. These plants, however, are an important biological component of many lakes (Wetzel 1964; Wetzel and Hough 1973). Except for the Lake Evaluation Index (Porcella et al. 1979), current methods use only the classical trophic state indicators of open-water nutrient concentrations, algal biomass, and transparency, which emphasize conditions in the pelagial zone. Even the Lake Evaluation Index, which includes a term for the percent macrophyte coverage, gives no consideration to nutrients, plant biomass, or production associated with macrophytes.

Errors in trophic state assessment will be small in lakes where macrophytes are confined to small littoral areas, but large errors can result in macrophyte-dominated lakes. This occurs because nutrient and chlorophyll concentrations can be low and Secchi disc transparency can be high in waters where there is an abundance of macrophytes. Under these conditions existing trophic classification systems would

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TABLE 1. Generalized trophic state classification standards (modified from Forsberg and Ryding 1980).

Trophic status	Total phosphorus ($mg \cdot m^{-3}$)	Total nitrogen ($mg \cdot m^{-3}$)	Chlorophyll *a* ($mg \cdot m^{-3}$)	Transparency (m)
Oligotrophic	<15	<400	<3	>4.0
Mesotrophic	15–25	400–600	3–7	2.5–4.0
Eutrophic	>25	>600	>7	<2.5

TABLE 2. Average chemical conditions for the surface waters of six Florida lakes between September 1979 and August 1980 (Canfield 1981).

Lake	pH	Total alkalinity ($mg \cdot L^{-1}$ as $CaCO_3$)	Total hardness ($mg \cdot L^{-1}$ as $CaCO_3$)	Total P ($mg \cdot m^{-3}$)	Total N ($mg \cdot m^{-3}$)	Chlorophyll *a* ($mg \cdot m^{-3}$)	Secchi depth (m)
Down	6.5	3	63	8	310	1.0	6.2
Fairview	8.0	52	65	15	450	2.5	4.8
Kerr	6.1	3	23	13	220	1.5	3.3
Lochloosa	7.4	23	31	36	1200	32	0.7
Okahumpka	8.3	50	60	14	880	5	1.2[a]
Stella	7.0	16	72	13	460	3	4.1

[a]Secchi depth represents bottom readings.

underestimate the lake's trophic status. For example, Secchi disc transparencies were greater than 5 m, total phosphorus concentrations averaged 11 $mg \cdot m^{-3}$, and chlorophyll *a* concentrations were less than 3 $mg \cdot m^{-3}$ in Lake Baldwin, Florida, when abundant growths (156 g dry $wt \cdot m^{-2}$) of hydrilla (*Hydrilla verticillata*) covered 80% of the lake's bottom (J. V. Shireman, unpublished data). For these conditions, trophic state index (TSI) values would be low and the lake would be classified as oligotrophic (Table 1) even though the abundance of hydrilla clearly demonstrates that the lake is productive. Current trophic classification systems only classified Lake Baldwin as eutrophic after the loss of hydrilla resulted in a structural and functional shift to plankton. Secchi disc transparencies decreased to less than 2 m, total phosphorus concentrations averaged 30 $mg \cdot m^{-3}$, and chlorophyll *a* values averaged 21 $mg \cdot m^{-3}$.

We propose, therefore, that as a preliminary approach the trophic status of lakes having growths of aquatic macrophytes may be assessed by adding the nutrients in the macrophytes to the nutrients in the water. This approach is consistent with Hutchinson's (1969) suggestion that trophic state determinations should be based on the total potential concentrations of nutrients in the lake, since low concentrations in the water may result because part of the lake's nutrient supply is located elsewhere (e.g. sediments or in the bodies of organisms such as macrophytes). It is also consistent with methods that use in-lake nutrient concentrations determined by nutrient loading, hydrology, and lake morphology as a major component of trophic state assessment (Dillon 1975; Vollenweider 1976). Our approach may also provide a basis for predicting the nutrient content and algal biomass of lakes when natural factors or management practices alter macrophyte abundance.

Materials and Methods

During September and October 1981 (the period of peak macrophyte abundance in Florida lakes), we sampled six Florida lakes with different limnological characteristics (Table 2) to determine the biomass of submersed aquatic macrophytes. In each lake, vegetation coverage was determined along transects that crossed different areas of the lake by use of a Raytheon DE-719 fathometer (Maceina and Shireman 1980). Along the fathometer transects, buoys (30–50 depending on lake size and the extent of macrophyte coverage) were placed in areas representing different macrophyte abundance. At each buoy, a single plant biomass sample was taken with a biomass sampler (Nall and Schardt 1978) modified to include an improved sampling bucket designed by the U.S. Army Engineer Waterways Experiment Station (Vicksburg, MS). Surface water (0.5 m) samples were collected randomly for determination of lake phosphorus concentrations. Phosphorus was emphasized as the criterion for trophic state assessment because phosphorus is often the limiting nutrient in lakes (Dillon and Rigler 1974; Jones and Bachmann 1976; Canfield 1981) and our study lakes had nitrogen–phosphorus ratios greater than 10 (Table 2), thus suggesting phosphorus limitation. Nitrogen, however, could be used in nitrogen-limited lakes (see Kratzer and Brezonik 1981). All water and plant samples were placed on ice until they could be analyzed the next day.

In the laboratory, plant samples were thoroughly rinsed, separated by species, and dried at 70°C to a constant weight. Each sample was weighed and plants were ground in a Wiley Mill until fragments were <0.85 mm. Phosphorus analysis of plant tissue (100 mg) included a 1-h digestion on a Tecam DG-1 digestion block at 350°C with a 1 mL of 20% H_2SO_4. After cooling, samples were reheated for 15 min with 1 mL of 30% H_2O_2. This procedure was repeated until the sample became clear. Total phosphorus concentrations were then determined with an ascorbic acid–molybdate reduction method modified from Mehlich (1978) and the American Public Health Association (1976). Surface water samples were analyzed for total phosphorus by using the procedures of Murphy and Riley (1962) with a persulfate digestion (Menzel

and Corwin 1965).

The total biomass of submersed aquatic macrophytes in each lake was determined by

$$(1) \quad TSMB = SA \times C \times B$$

where TSMB = total submersed macrophyte biomass (kilograms), SA = lake surface area (square metres), C = percent cover of submersed aquatic macrophytes, and B = average macrophyte biomass collected with the biomass sampler (kilograms per square metre). The value C was calculated from the fathometer transect data by

$$(2) \quad C = \sum_{a=1}^{N} (WF_a \times \%TC_a)$$

where WF = individual transect length (metres) divided by the sum of all transect lengths (metres) and %TC = vegetated length of transect (metres) divided by the transect length (metres). To determine the quantity of phosphorus contained in the macrophyte beds of each lake, we first estimated the biomass of the individual species by multiplying our estimates of total submersed macrophyte biomass by the proportion each individual species contributed to the samples taken with the biomass sampler. We then multiplied the biomass estimates of the individual species by the average phosphorus content of the species, as determined by our tissue analyses. Values are given in Table 3. These estimates were summed to obtain a value for the total amount of phosphorus associated with macrophytes in the lake. To estimate the total phosphorus content of the water column (WCP values), mass balance calculations were made by using measured lake volume, the phosphorus content of the water, and the phosphorus content of the macrophytes assuming 100% decomposition (Jewell 1971; Hill 1979) and recycling into the water column. Although there are errors associated with the measurement of total phosphorus in the water and plants, the largest source of error in estimating WCP values is generally associated with the estimate of macrophyte biomass. To calculate empirical 95% confidence limits for our WCP values, we assumed that all the error was in the estimate of total submersed macrophyte biomass. Phosphorus content of the sediments was not considered.

Results and Discussion

In our lakes, total submersed macrophyte biomass ranged from 18 100 kg dry wt in Lake Kerr to 2 170 000 kg dry wt in Lake Lochloosa (Table 4). For our calculated potential water column phosphorus concentrations, 20–96% of the phosphorus was in the submersed macrophytes and WCP values were 1.2–26 times the measured open-water concentrations (Table 4). Based on these data, there is considerable organic matter and nutrients associated with aquatic macrophytes. The effect of these macrophytes on WCP values and, therefore, trophic state assessment depends on the amount of macrophytes relative to the total lake volume. For example, Lake Fairview has extensive growths (49 g dry wt·m^{-3}) of hydrilla, pondweed (*Potamogeton illinoensis*), and stonewort (*Nitella* sp.). Using our measured open-water total

TABLE 3. Comparison of lake macrophyte species. B, individual species biomass in kg dry wt; %P, percent phosphorus content; P, phosphorus standing crop in kg; NC, not collected.

Macrophyte species	Lake																	
	Down			Fairview			Kerr			Lochloosa			Okahumpka			Stella		
	B	%P	P	B	%P	P	B	%P	P	B	%P	P	B	%P	P	B	%P	P
Hydrilla verticillata	NC	—	—	134 000	0.14	188	9 290	0.40	37	2 170 000	0.26	5 640	492 000	0.21	1 033	138 000	0.13	179
Najas guadalupensis	NC	—	—	253	0.11	0.28	NC	—	—	NC	—	—	NC	—	—	NC	—	—
Ceratophyllum demersum	NC	—	—	8	0.22	0.02	417	0.41	1.7	NC	—	—	255	0.22	0.56	612	0.19	1.2
Potamogeton illinoensis	NC	—	—	49 800	0.14	70	NC	—	—	NC	—	—	4 640	0.17	7.9	NC	—	—
Vallisneria americana	NC	—	—	NC	—	—	NC	—	—	NC	—	—	2 720	0.20	5.4	83	0.29	0.24
Mayaca aubletii	82 600	0.16	132	NC	—	—	3 860	0.26	10	NC	—	—	NC	—	—	NC	—	—
Bacopa caroliniana	NC	—	—	NC	—	—	3 410	0.35	12	NC	—	—	NC	—	—	NC	—	—
Egeria densa	NC	—	—	NC	—	—	18	0.17	.03	NC	—	—	NC	—	—	NC	—	—
Myriophyllum pinnatum	NC	—	—	NC	—	—	326	0.17	.55	NC	—	—	NC	—	—	NC	—	—
Eleocharis baldwinii	NC	—	—	NC	—	—	561	0.38	2.1	NC	—	—	NC	—	—	NC	—	—
Sagittaria subulata	NC	—	—	1 000	0.13	1.3	235	0.53	1.3	NC	—	—	NC	—	—	NC	—	—
Nitella sp.	NC	—	—	25 000	0.16	40	NC	—	—	NC	—	—	NC	—	—	NC	—	—
Filamentous algae	166	0.05	0.08	463	0.13	0.60	NC	—	—	NC	—	—	NC	—	—	NC	—	—

TABLE 4. Comparison of total submersed macrophyte biomass (TSMB), total submersed macrophyte phosphorus (TSMP), surface area (SA), volume (V), measured total phosphorus concentration (TP), potential water column phosphorus assuming 100% release of phosphorus from the macrophytes (WCP), and macrophyte concentration (TSMB·V^{-1}) measured in six Florida lakes during September–October 1981. Numbers in parentheses for TSMB are 95% confidence intervals. For other variables, numbers represent empirical 95% confidence intervals calculated assuming all errors are associated with measurements of TSMB.

Variable	Lake					
	Kerr	Down	Stella	Lochloosa	Fairview	Okahumpka
TSMB (kg dry wt)	18 100 (±6100)	82 800 (±17 700)	139 000 (±30 000)	2 170 000 (±530 000)	211 000 (±48 500)	500 000 (±118 000)
TSMP (kg)	65 (±22)	132 (±28)	180 (±39)	5 640 (±1380)	300 (±69)	1 050 (±250)
SA (ha)	1 130	360	123	2 190	114	208
V (m^3)	42 000 000	12 000 000	4 300 000	46 000 000	4 300 000	2 600 000
TP (mg·m^{-3})	8	9	12	25	10	16
WCP (mg·m^{-3})	9.6 (±0.5)	20 (±2)	54 (±9)	148 (±30)	80(±16)	420 (±96)
TSMB·V^{-1} (g dry wt·m^{-3})	0.4 (±0.2)	7 (±1)	32 (±7)	47 (±12)	49 (±11)	192 (±46)

phosphorus concentrations (10 mg·m^{-3}) and the criteria in Table 1, the lake would be classified as oligotrophic and have a Carlson (1977) TSI value of 37. By use of our calculated WCP value (80 mg·m^{-3}), however, the lake would be classified as eutrophic and have a Carlson (1977) TSI value of 67, which is similar to other lakes located in the same physiographic region (Canfield 1981). In contrast, macrophyte abundance in Lake Kerr is negligible (0.4 g dry wt·m^{-3}). If the phosphorus contained in the macrophytes was released to the open water the WCP value would only be 1.6 mg·m^{-3} higher than the measured total phosphorus concentration of 8 mg·m^{-3} (Table 4). This would not appreciably alter the lake's trophic state classification.

To determine if our calculated WCP values provide reasonable estimates of open-water phosphorus concentrations when macrophyte abundance is low, we compared our WCP values to open-water phosphorus concentrations measured in other lakes located in the same physiographic region (Table 5). We made this comparison because studies of regional limnology have demonstrated relationships between regional physiography and surface geology (edaphic factors) and the chemical composition and productivity of lakes located in different lake districts (Deevey 1940; Moyle 1956; Jones and Bachmann 1978). In each region, maximum measured phosphorus values are from lakes with low macrophyte abundance. With the exception of Lakes Okahumpka and Stella, WCP values are within the range of measured open-water phosphorus values and generally similar to the phosphorus-rich lakes that have few macrophytes. Lake Stella is the only lake in its region receiving urban runoff, which may account for the WCP value being higher than observed phosphorus concentrations. We do not know why the WCP value in Lake Okahumpka is greater than maximum phosphorus values in the region, but Lake Okahumpka is situated in an area of poorly drained, nutrient-rich organic soils. Where these soils occur in Florida, phosphorus values similar to Lake Okahumpka's WCP concentrations can be found (U.S. Environmental Protection Agency 1978; Canfield 1981), which indicates that the calculated value may not be unreasonable.

We also compared our predicted WCP value with the measured open-water phosphorus concentration in Lake Baldwin, Florida, where submersed macrophytes were removed by use of grass carp (*Ctenopharyngodon idella*). In 1978, Lake Baldwin supported approximately 100 000 kg dry wt of hydrilla, which contained 140 kg of phosphorus (Shireman and Maceina 1981; J. V. Shireman, unpublished data). Open-water phosphorus values averaged 11 mg·m^{-3}. Based on these data, the WCP value for Lake Baldwin would be 52 mg·m^{-3}. After hydrilla was virtually eliminated by the grass carp, the open-water phosphorus concentration in the lake averaged 30 mg·m^{-3}, substantially lower than the calculated WCP value. However, our predicted phosphorus concentration did not account for the phosphorus retained by the grass carp (72 kg) (J. V. Shireman, unpublished data). Correcting for this, Lake Baldwin's WCP value would be 31 mg·m^{-3}, which agrees with the measured phosphorus concentration.

From these data and those in Tables 4 and 5, we suggest that the importance of using WCP values to evaluate the

TABLE 5. Comparison of potential water column total phosphorus concentrations (WCP) for the study lakes with measured phosphorus concentrations in lakes located in the same geologic and physiographic region. Data taken from Canfield (1981). Numbers in parentheses are empirical 95% confidence limits (see Table 4). *N* is number of lakes sampled.

	Phosphorus concentrations ($mg \cdot m^{-3}$)			
		Observed in other lakes		
Lake	WCP	Minimum	Maximum	*N*
Kerr	9.6 (±0.5)	0.1	35	4
Down	20 (±2)	2.1	25	8
Stella	54 (±9)	0.5	25	4
Fairview	80 (±16)	3.7	98	8
Lochloosa	148 (±30)	10	209	28
Okahumpka	420 (±96)	1.0	54	5

trophic status of lakes having aquatic macrophytes is directly related to the macrophyte abundance per volume of lake or epilimnion (our lakes were not thermally stratified). Our analysis indicates that macrophytes have little effect on trophic state assessment when <25% of the phosphorus in the water column is associated with macrophytes and the mean macrophyte concentration in the lake is less than 1 g dry $wt \cdot m^{-3}$ (Table 4). We cannot at this time, however, provide definitive criteria for when WCP values should be considered in lake assessment. Until more lakes are sampled to provide such criteria, we believe that decisions to use WCP values should be made on the basis of the extent of macrophyte coverage (percent of surface area) in relation to lake volume. For large deep lakes with small littoral areas, the effect of macrophytes on the assessment of lake trophic state will be negligible. Our approach, however, is likely to be most useful when classifying shallow macrophyte-dominated lakes.

There are, however, several problems associated with the use of WCP values. Similar to other classification systems based on a single criterion, information on the structural and functional characteristics of the biotic community may be lost when multivariate observations are summarized by a single parameter. This can be especially important when considering aquatic macrophytes because these plants have a different effect on lake productivity, nutrient cycling, and perceived trophic state characteristics than do phytoplankton. Another problem is that our approach may overestimate the trophic status of some lakes. Certain macrophytes can mobilize phosphorus from the sediments (Carignan and Kalff 1980). If these plants transport nutrients deposited during earlier periods of high nutrient loading into the stems and leaves, our trophic state assessment would not match assessments based on current nutrient loading rates. We also assumed that 100% of the phosphorus in the macrophytes would be released to the overlying water. Phosphorus release from macrophytes during die-off and decomposition, however, need not be 100% (Landers 1982); thus, phosphorus concentrations in the water following a reduction in macrophyte abundance may be less than calculated WCP values. Estimating WCP values is also a labor-intensive process (accurate measures of macrophyte biomass requires the collection of numerous samples) that is inconsistent with current approaches to trophic state classification, which require minimal data (Carlson 1977; Kratzer and Brezonik 1981; Osgood 1982).

Despite the potential problems of using WCP values, we know of no simple quantitative method for assessing the trophic status of lakes having growths of aquatic macrophytes. Until research can develop a simpler alternative, we feel that our approach reduces the danger that inappropriate assessments of trophic status will be made for macrophyte-dominated lakes. This is especially important because regulatory and management decisions are often made using open-water nutrient, chlorophyll *a*, and Secchi disc transparency data obtained from surveys of regional limnology. Values for WCP may also prove useful for predicting the impact of changes in macrophyte abundance on limnological characteristics when the nutrient supply to the lake remains unchanged. Currently, there is no method to evaluate how open-water nutrient concentrations, chlorophyll *a* values, and Secchi transparencies will change with partial to complete removal of macrophyte biomass by natural factors or management practices (harvesting, herbicides, or herbivores). Using WCP values in conjunction with simple empirical nutrient–chlorophyll and chlorophyll–Secchi models (Dillon and Rigler 1974; Jones and Bachmann 1976, 1978; Smith 1982) may provide the quantitative approach needed to estimate a lake's response to a given level of macrophyte removal.

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Daily Mortality Rates of Larval and Juvenile American Shad (*Alosa sapidissima*) in the Connecticut River with Changes in Year-Class Strength

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CRECCO, V., T. SAVOY, AND L. GUNN. 1983. Daily mortality rates of larval and juvenile American shad (*Alosa sapidissima*) in the Connecticut River with changes in year-class strength. Can. J. Fish. Aquat. Sci. 40: 1719–1728.

Age-specific growth and survival rates were estimated for larval and juvenile American shad (*Alosa sapidissima*) from the Connecticut River from 1979 to 1982. Relative indices (CPE) of year-class strength of juveniles determined from seine sampling in 1978–82 and 1966–73 are compared with resulting levels of adult recruitment. Length–age data for larval and juvenile American shad were determined from sagittal otoliths. Length increments among larval and juvenile shad followed an asymptotic pattern with age, both life stages being well described by the Gompertz equation. Larval survivorship curves from 1979 to 1982 were age specific, with mortality rates of 19.8–25.6%/d for first feeding larvae and 4.3–8.7%/d for larvae approaching metamorphosis. By contrast, juvenile mortality rates were much lower (1.8–2.0%/d) and more consistent among years. Juvenile indices of year-class strength from 1966 to 1973 were positively correlated ($r = +0.92$, df 7, $P < 0.001$) with recruitment levels of adult females 4–6 yr later, suggesting that year-class strength of shad is established prior to the juvenile stage.

CRECCO, V., T. SAVOY, AND L. GUNN. 1983. Daily mortality rates of larval and juvenile American shad (*Alosa sapidissima*) in the Connecticut River with changes in year-class strength. Can. J. Fish. Aquat. Sci. 40: 1719–1728.

La croissance et les taux de survie particuliers à l'âge ont été estimés chez des aloses savoureuses (*Alosa sapidissima*) larvaires et juvéniles capturées dans la rivière Connecticut de 1979 à 1982. Les indices relatifs (PUE) d'abondance des classes de juvéniles, déterminés par échantillonnage de poissons capturés à la senne en 1978–82 et 1966–73, ont été comparés aux niveaux de recrutement d'adultes qui en ont résulté. Les otolithes sagittaux ont servi à l'établissement des données longueur–âge des aloses larvaires et juvéniles. Les augmentations de longueur chez ces aloses suivent une courbe asymptotique en fonction de l'âge, l'équation de Gompertz décrivant adéquatement l'un et l'autre stade du cycle de vie. Les courbes de survie des larves entre 1979 et 1982 sont particulières à l'âge, les taux de mortalité de ces dernières au début de l'alimentation étant de 19,8–25,6 %/jour et, pour les larves approchant la métamorphose, de 4,3–8,7 % par jour. Par contraste, les taux de mortalité des juvéniles sont beaucoup plus faibles (1,8–2,0 %/jour) et plus uniformes d'une année à l'autre. Il y a corrélation positive entre les indices d'abondance des classes des juvéniles de 1966 à 1973 ($r = +0,92$, dl 7, $P < 0,001$), d'une part, et les niveaux de recrutement des femelles adultes 4–6 ans plus tard, d'autre part. Ceci donne à penser que les effectifs de classes d'âge des aloses sont déterminés avant le stade juvénile.

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EFFECTIVE management of anadromous herring such as American shad, *Alosa sapidissima*, depends on the ability to predict whether egg production in any given year will ensure adequate future recruitment (Fredin 1954; Leggett 1976; Crecco et al. 1981). Unfortunately, the emergence of strong year-classes of many herring fishes is not assured by high egg production, nor are weak year-classes a consequence of low egg production (Ricker 1962; Dragesund and Nakken 1973; Gulland 1973). The fact that strong year-classes of American shad occasionally arise from small parent stocks suggests that year-class strength is established by differential mortality during the prerecruitment phase. Therefore, it would be useful to measure prerecruit mortality over the long term and identify the life stage(s) in which year-class strength is established. No data are presently available on embryonic, larval, or juvenile mortality rates of American shad to examine these prerecruit processes.

Relatively few attempts have been made to measure larval and juvenile mortality directly in the wild. May (1974) and, more recently, Dahlberg (1979) reviewed the available studies on larval survivorship and found that most curves were difficult to interpret because of sampling biases and

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questionable methods by which larval growth rates were estimated. The discovery of daily growth rings on the otoliths of young fish (Pannella 1971) has made it possible to describe age-specific larval and juvenile growth rates, thus allowing more accurate survivorship curves.

One aspect of the early life history of American shad that makes this species particularly suited for estimating age-specific survival rates is that both larval and juvenile shad are associated with specific habitats such as eddies and backwater areas from which they can be effectively sampled with a plankton bag seine (Mitchell et al. 1925; Cave 1978).

This paper presents age-specific mortality estimates of Connecticut River American shad from yolk absorption through juvenile development for the period 1979–82. Weekly zooplankton densities are also presented from May through July and related to changes in larval mortality and year-class strength from 1979 to 1982. The relationship between juvenile indices of abundance from 1966 to 1973 and resulting year-class recruitment to the adult American shad runs is analyzed to determine the life stage(s) in which year-class strength is established.

Materials and Methods

The term shad "larva" is defined here as any pre-metamorphosed shad between 6 and 25 mm (total length). American shad larvae were sampled during daylight in the Connecticut River with a 6.1-m plankton bag seine (2.4 m deep, wing and bag mesh of 0.505 mm) and 30-m lead ropes from May 15 to July 15, 1979–82. One seine haul was taken weekly at each of 12 sites located north of the Enfield Dam (Fig. 1). A pilot study conducted in 1978 showed that few shad larvae were taken from seine sites below the Enfield Dam (V. A. Crecco, unpublished observations). All seine sites were chosen within eddies and backwater areas where shad larvae are known to occur (Cave 1978).

The seine bag had a funnel-like shape to which a plankton bucket (0.250-mm mesh) was attached to facilitate removal of larvae from the net. The seine was set from the boat about 30 m offshore and slightly upriver of each site and then towed by the boat in a downstream arc toward shore and beached using the ropes. Approximately 10–20 larvae were randomly selected from each sample and frozen for otolith age determinations. All remaining larvae were washed into the plankton bucket and fixed in 4% formalin.

Juvenile American shad were collected weekly from July 15 to October 15, 1978–82 at seven stations (Fig. 1) below the Holyoke Dam. Juvenile sampling occurred during daylight hours with a 15.2-m nylon bag seine (4.8-mm mesh, 2.4 m deep, 2.4-m bag) and 30-m lead ropes similar to that used in a previous juvenile survey (Marcy 1976). One seine haul was completed at each station using the procedures described previously for larval sampling.

The composition and abundance of river zooplankton were monitored weekly from May 15 to July 15, 1979–82 at four of the larval seine stations (Fig. 1). Zooplankton were sampled with a 13.0-cm Clark–Bumpus plankton sampler fitted with an 80-μm mesh net. Duplicate 1-min tows were made in a downstream direction 1 m below the surface. Mean density (number per cubic metre) of each sample was estimated by direct proportion between the mean number of organisms counted in two to three aliquots and the volume of river water sampled. Only cladocerans, copepods, and immature insects were tabulated, as shad larvae feed almost exclusively on these prey (Maxfield 1953; Domermuth 1976). The mean and standard deviation of weekly zooplankton densities were compared among the 1979–82 year-classes. This analysis was designed to determine the relationship among zooplankton densities, larval mortalities, and year-class strength.

FIG. 1. Location of larval and juvenile seine and zooplankton sampling stations on the Connecticut River.

Larval and juvenile American shad were distinguished from their congeners, the blueback herring, *Alosa aestivalis*, and alewive, *Alosa pseudoharengus*, based on the criteria reported by Leim (1924), Lippson and Moran (1974), and Marcy (1976). All larvae and juveniles were counted and measured to total length (millimetres) whenever possible. Where direct enumeration was impractical, as for samples containing many (>1000) larvae, the number of shad was determined indirectly. From 1979 to 1980, a gravimetric method was used to estimate larval abundance (N_{ij}) as follows:

$$(1)\quad N_{ij} = \frac{b_{ij}h_{ij}}{W}$$

where b_{ij} = number of larvae counted from the subsample of

the ith sample from the jth collection date, h_{ij} = total weight (0.01 mg) of larvae from the entire sample, and W = weight of the larval subsample. In 1981–82, a Folsom plankton splitter was used to partition large samples into four to eight equal subsamples. The total sample size was estimated by counting the number of larvae in one subsample and multiplying that value by the number (four to eight) of subsamples. Guelpen et al. (1982) reported that the Folsom plankton splitter was the most accurate and precise method of subsampling larval fish. In both cases, all larvae in the subsample were measured (millimetres) and the length frequency distribution extrapolated to the entire sample.

Approximately 50–75 fish from each of the weekly collections were examined for age and growth analyses. Otoliths were not removed from juveniles in 1978; thus, no juvenile age, growth, or mortality estimates could be made. Larval age (days) was estimated by counting growth rings on sagittal otoliths (Pannella 1971; Brothers et al. 1976), which were embedded in mounting medium. By contrast, otoliths from preserved juvenile American shad were etched in 1% solution of HCl for 1 min, rinsed in distilled water, and allowed to dry before being cleared in immersion oil for 7–10 d. The crystalline nature of juvenile otoliths allows preservation in formalin without dissolution. Daily growth rings were counted three times under transmitted light (100×), and the final age was regarded as the mean of the three estimates. Otolith half-length and distance from the focus to each seventh growth ring were measured (micrometres). Back calculated lengths (millimetres) were estimated for each 7-d interval by the Lea method (Ricker 1975).

Knowledge of age-specific growth of larval and juvenile American shad is important for constructing survivorship curves. Farris (1960) showed that the shape of larval survivorship curves depends on whether larval length increments are linear, exponential, or asymptotic. In this study, length–age data for each year were recorded from hatching through juvenile development and fitted to the exponential, Gompertz, and von Bertalanffy growth equations by various methods (Laird et al. 1965; Bayley 1977; Kaufmann 1981). The mathematical equation that best depicted age-specific growth patterns was also used to construct larval and juvenile survivorship curves by the method of Sette (1943). All seine-caught larvae taken annually between 10 and 25 mm were separated into a number of 1-mm length groups and the average age (days) of each length group was estimated by solving the appropriate growth equation with respect to age (Lough 1976). All juvenile American shad taken annually between 40 and 80 mm were separated into a number of 3-mm length groups and the average age of each length group was determined by rearranging the appropriate growth equation. Prejuveniles between 26 and 39 mm were not included in the survival analysis because most were not retained fully in the mesh (4.8 mm) of the juvenile bag seine.

Linear regression analysis was used to estimate instantaneous mortality rates for the following length intervals: (1) 10–13 mm, representing first-feeding larvae (Maxfield 1953), (2) 13–18 mm, signifying intermediate-sized larvae, (3) 18–21 and 21–25 mm, representing advanced larvae, and (4) 40–80 mm, representing the length range that includes most juvenile American shad captured. The natural

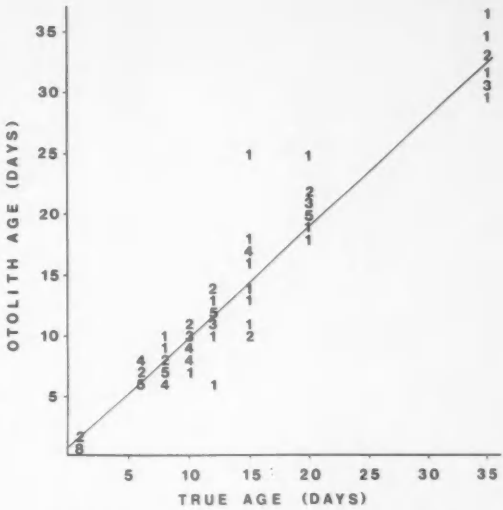

FIG. 2. Otolith age versus true age of American shad larvae (numbers indicate number of observations at each age).

logarithm of abundance for larval American shad at each 1-mm length class was linearly regressed against its corresponding age. The same procedure was used for juvenile American shad except that logarithm abundance was derived for a number of 3-mm length classes. The resulting equation was calculated for each of the above length intervals from 1979 to 1982:

$$(2) \quad \ln N_t = ae^{-Z_t}$$

where Z_t = slope of the regression and is defined as instantaneous mortality rate for the entire length interval, N_t = predicted number of fish at age t, and a = y-axis intercept. The instantaneous daily mortality rate (n_t) for each length interval was then determined by

$$(3) \quad n_t = Z/t_{\max}$$

where $t_{\max}$ = total number of days between the beginning and end of each length interval, from which the daily mortality rate (M_t) (percent per day) was calculated by

$$(4) \quad M_t = 1 - e^{-n_t}.$$

Accurate estimates of daily mortality rates depend on the assumption that shad larvae of all sizes are equally susceptible to seine sampling. The seine used in this study was able to capture relatively few sac larvae between 7 and 9 mm. Therefore, it is essential to discuss the potential causes for undersampling prolarvae and make necessary adjustments in future surveys. The potential sources of bias include one or more of the following: (1) escapement of sac larvae through the seine mesh (Lenarz 1972), (2) active evasion of larvae away from the seine (Barkley 1972), and (3) differences in the vertical and horizontal distribution of pro- and post-larvae (Cassie 1963). Extrusion of sac larvae through the seine mesh is not

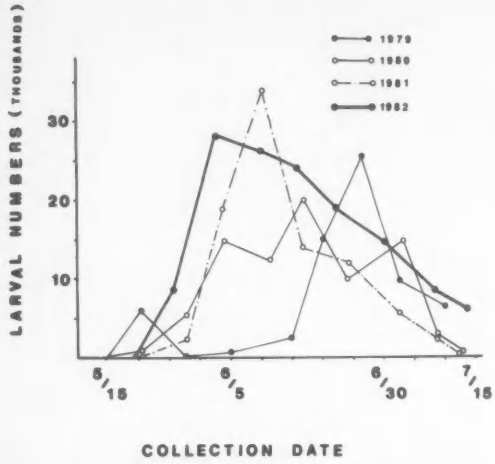

FIG. 3. Temporal changes in the total number of seine-caught shad larvae from 1979 to 1982.

expected because the maximum widths (0.75–1.00 mm) of prolarval American shad are much wider than the mesh size (0.505 mm). The second factor, the ability of prolarvae to maneuver around a 6.2-m plankton seine, is unlikely since most studies (Rosenthal and Hempel 1970; Rosenthal 1970; Blaxter and Staines 1971) have shown that prolarvae of most herring species are weak swimmers. The final explanation, differences in the distribution of pro- and post-larvae, provides the best explanation. Layzer (1974) and Marcy (1976) noted that American shad ova are semibuoyant and drift along the river bottom. Newly hatched American shad larvae also remain near the bottom until the yolk is nearly gone (Mitchell et al. 1925), after which they swim near shore and become susceptible to seine sampling. Therefore, it is reasonable to assume that most prolarvae remain in relatively deep water (>3 m) where they are less available to capture.

Another potential source of bias is gear avoidance by larger (>17 mm) larvae (Tranter 1968) due to their improved swimming ability. If gear avoidance is a problem, the number of American shad larvae should diminish sharply with size, causing mortality estimates to increase with age. The extent of gear avoidance will be addressed later. Perhaps the most difficult problem in obtaining a representative sample of shad larvae is the effect of spatial heterogeneity (Cassie 1963; Wiebe 1970). A patchy distribution is characteristic of most plankton populations and usually results in high variation in larval catches among successive samples. In this study, the effect of spatial heterogeneity was minimized by sampling preferred habitats for larval American shad over a relatively short duration (weekly).

The ability to accurately age larval and juvenile American shad with otoliths depended on the following assumptions: (1) that each growth ring is deposited daily and (2) that the initial ring formation occurs shortly after hatching. To test these assumptions, otolith age determinations were made in 1982 on 97 hatchery-reared American shad larvae from the Lamar National Fish Hatchery, Lamar, PA. Both sagittal otoliths were removed from fish ranging from 7.0 to 22.0 mm total length and were aged in the same manner as American shad larvae from the Connecticut River. The true age and length of the hatchery fish were unknown to the observer while aging the fish. The average number of sagittal rings was linearly related to the true daily age (Fig. 2). The estimate of the slope (0.928) did not differ significantly from 1.0 ($t = 0.63$, $P < 0.50$), indicating that the chronological ages from the otoliths were similar to the true ages. Moreover, eight of ten 1-d-old fish were aged accurately by the otolith method, suggesting that the first growth ring is deposited shortly after hatching.

TABLE 1. Juvenile relative index of abundance from 1966 to 1973 and from 1978 to 1982 compared with the estimated number of virgin female shad from the 1966–77 year-classes.

Year	Juvenile index of year-class strength[a]	Virgin female recruitment[b] in $t + 4$, $t + 5$, and $t + 6$
1966	12.8	258 581
1967	20.2	209 184
1968	11.1	163 908
1969	19.0	248 047
1970	27.8	293 386
1971	65.7	459 330
1972	15.3	269 518
1973	12.4	168 052
1974[b]	—	304 343
1975	—	254 895
1976	—	275 381
1977	—	381 438
1978	27.2	—
1979	19.6	—
1980	42.7	—
1981	16.0	—
1982	4.7	—

[a]Juvenile indices unavailable for 1974–77.
[b]Adult recruitment defined as the sum of virgin female shad of year-class (t) in years $t + 4$, $t + 5$, and $t + 6$.

The relative strength of the 1978–82 year-classes was represented by the mean catch per effort (CPE) of juvenile shad from July 15 to October 15 (Crecco et al. 1981) and compared with those from a previous juvenile survey from 1966 to 1973 (Marcy 1976). Because the juvenile indices reported by Marcy (1976) were computed from 16 seine stations, these indices were recalculated based on the 7 stations whose positions on the river most closely resembled our stations (Fig. 1).

The relationship between juvenile year-class strength and subsequent recruitment to the adult runs was examined by regression analyses. Year-class strength of adult American shad was derived from spawning history, age structure, and population estimates for the years 1966–82 (Leggett 1976; Jones et al. 1976; Crecco et al. 1981). The adult index is defined as the contribution of virgin female American shad of year-class (t) in the spawning runs during years $t + 4$, $t + 5$, and $t + 6$. Data for male American shad were not used because male population estimates and age structure data are severely biased by gill net selectivity (Fredin 1954; Crecco et al. 1980).

TABLE 2. Estimates of parameters for the Gompertz equations, 1979–82. L_o = average length of a newly hatched shad larva (7.0 mm), $K = -\ln 7.0/25.0$ where 25.0 mm is L_∞, the average length of a shad larva at metamorphosis, $a = \{\ln K - \ln [-\ln (L_t/L_\infty)]\}/t$ where t = age of the fish, $L_t = L_o e^{K(1-e^{-at})}$, and r^2 = coefficient of determination.

Year	Sample size	L_o	L_∞	K	a	r^2
American shad larvae						
1979	146	7.0	—	1.273	0.0754	0.993
1980	140	7.0	—	1.273	0.0694	0.982
1981	147	7.0	—	1.273	0.0690	0.991
1982	158	7.0	—	1.273	0.0645	0.988
American shad juveniles						
1979	105	30.0	99.0	1.194	0.0364	0.930
1980	117	30.0	92.0	1.121	0.0504	0.887
1981	75	30.0	87.0	1.065	0.0526	0.830
1982	106	30.0	106.0	1.262	0.0349	0.833

Results

Relative Abundance of Larvae and Juveniles

The distribution and number of seine-caught larvae differed among the 4 years (Fig. 3). Of the 69 408 American shad larvae collected during 1979, only 10.8% (7496 fish) were captured before May 30, while 84.8% (58 580 fish) were collected between June 21 and mid-July. By contrast, over 90 000 American shad larvae were captured annually in 1980, 1981, and 1982, with most larvae being taken in June. These data show that June is the month during which most larval American shad emerge.

The relative strength of the 1978–82 year-classes was represented by juvenile CPE data from July 15 to September 15 and compared with juvenile indices for the years 1966–73 and corresponding adult recruitment (Table 1) (Crecco et al. 1980). The 1980 year-class was 2.2 and 2.7 times greater than the 1979 and 1981 year-classes, respectively, and 57% larger than the 1978 year-class. Except for the outstanding 1971 year-class, the 1980 cohort is the strongest year-class and the 1982 year-class is the weakest for which data are available. There was a significant ($r = +0.92$, df 7, $P < 0.001$) positive correlation between the juvenile indices from 1966 to 1973 and the resulting adult recruitment from these year-classes. It is evident that the strong 1971 year-class, manifested initially during juvenile development, also produced the highest number of virgin recruits 4–6 yr later. Similarly, relatively weak year-classes such as the 1968 and 1973 cohorts were also relatively weak in the adult runs. Since juvenile indices of abundance provide an accurate qualitative prediction of future adult recruitment, the differential mortality rates that establish strong or weak year-classes probably occur prior to the juvenile stage.

Larval and Juvenile Growth

A count of otolith rings indicated that first-feeding larvae (10–13 mm) were between 4 and 9 d old. Since shad larvae between 7 and 10 mm exhaust the yolk sac approximately 3–6 d after hatching (Leim 1924; Maxfield 1953; Marcy 1976), this suggests that the first growth ring for Connecticut River shad larvae is deposited shortly after hatching. Age-specific growth of American shad larvae approximated an asymptotic relationship in which length increments were nearly linear from hatching until about 20 d old, followed by a 10-d period of declining growth rates as larvae approach metamorphosis (30 d old) (Table 2). After metamorphosis, juvenile shad apparently undergo a second asymptotic growth phase, as indicated by the linear increase in length from 30 to 70 d, with daily length increments declining slowly to a theoretical asymptote (87–106 mm) at about 75–100 d old.

The von Bertalanffy, exponential, and Gompertz growth equations were fitted to length–age data of larval and juvenile shad, but the Gompertz function provided the best overall

TABLE 3. Comparison between observed mean lengths (mm) of larval and juvenile American shad and those predicted from the Gompertz growth equations, 1979–82. Observed mean lengths were back-calculated from otolith growth rings. Lengths of larvae from 1 to 28 d old were predicted by the Gompertz equation: $L_t = L_o e^{K(1-e^{-at})}$. Lengths of juveniles from 35 to 84 d old were predicted by $L_t = L_o e^{K(1-e^{-a(t-35)})}$.

	1979		1980		1981		1982	
Age (d)	Observed	Predicted	Observed	Predicted	Observed	Predicted	Observed	Predicted
1	7.8	7.7	7.2	7.6	7.9	7.6	7.2	7.6
7	12.1	11.8	12.0	11.4	11.5	11.4	11.2	11.1
14	17.0	16.1	15.6	15.4	15.9	15.4	15.0	14.9
21	19.6	19.3	19.0	18.6	18.8	18.5	18.1	18.0
28	23.0	21.4	19.9	20.8	21.7	20.8	20.2	20.3
35	33.0	31.3	31.5	31.7	31.7	31.7	34.7	31.3
42	42.2	39.2	43.6	41.9	42.9	41.6	38.2	39.4
49	50.8	48.3	52.6	52.9	51.7	52.3	48.9	48.9
56	60.9	56.8	60.6	62.4	61.2	61.1	56.7	57.8
63	69.1	64.3	68.3	70.0	69.8	68.2	61.9	65.9
70	73.6	70.9	74.4	76.0	76.8	73.5	67.5	73.1
77	79.2	76.4	80.1	80.4	80.0	77.4	78.3	79.2
84	82.0	81.0	84.8	83.7	82.0	80.3	84.7	84.3

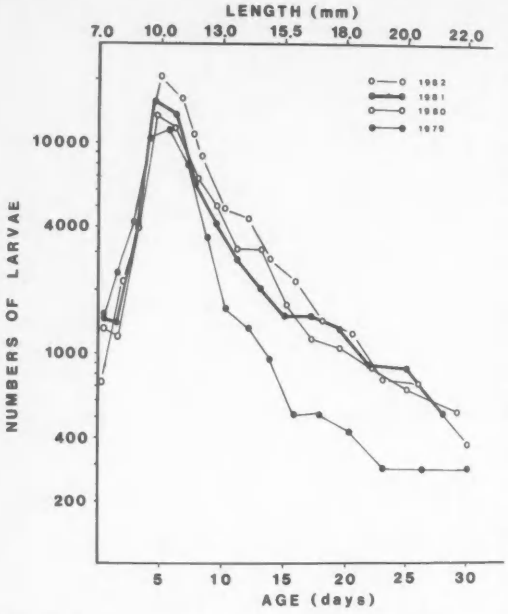

FIG. 4. Survivorship curves for seine-caught shad larvae between 7 and 25 mm, 1979–82.

description of age-specific growth (Table 3). According to the Gompertz equation, shad larvae during 1979–82 grew between 0.7 and 0.9 mm/d from hatching to about 20 d old, after which daily length increments diminished to about 0.3–0.5 mm/d. By contrast, juvenile shad grew about 1.2–1.4 mm/d between 30 and 60 d old, then daily growth in length decreased to about 0.8–0.9 mm/d between 60 and 90 d old.

LARVAL AND JUVENILE MORTALITY

The overall trend in age-specific survival was similar from 1979 to 1982 (Fig. 4), with larval mortality rates being highest among first-feeding larvae (10–13 mm) and lowest among larvae approaching metamorphosis. It is also clear that larval shad between 7 and 9 mm were sampled incompletely, as evidenced by the ascending left limb of each catch curve. These data indicate that the magnitude of larval mortality between 10 and 25 mm is a declining function of age, demonstrating that the probability of surviving to metamorphosis depends largely on whether a larva can survive the first 8–12 d after exogenous feeding begins.

While the larval survivorship curves were similar in general shape from 1979 to 1982, the magnitude of mortality between various length intervals differed among the 4 yr (Table 4). Daily mortality rates among first-feeding larvae (10–13 mm) were lowest (19.8%/d) for the strong 1980 year-class while being almost identical for the weaker 1979 (25.4%/d), 1981 (25.6%/d), and 1982 (25.0%/d) year-classes. However, mortality rates among the other larval length intervals showed

TABLE 4. Age-specific larval mortality rates (M) based on 10 000 larvae at 4 d old, 1979–82. Age was determined by rearranging the Gompertz equation: $t = \ln\{K/[K - \ln(L_t/L_0)]\}/a$, where L_t = observed length.

Length group (mm)	Age (d)[a]	No. surviving	M (%/d)	Equation	Correlation coefficient r
			1979		
10.0	4.3	10 000[a]	25.4	$\ln N_t = 52\,317.37e^{-0.293t}$	−0.941
13.0	8.8	2 699	18.3	$\ln N_t = 15\,835.75e^{-0.202t}$	−0.954
18.0	17.9	426	8.2	$\ln N_t = 2\,398.71e^{-0.086t}$	−0.933
21.0	26.3	208	4.3	$\ln N_t = 957.14e^{-0.044t}$	−0.875
23.0	30.1	176			
			1980		
10.0	4.7	10 000	19.8	$\ln N_t = 41\,280.68e^{-0.221t}$	−0.979
13.0	9.5	3 422	14.4	$\ln N_t = 19\,648.75e^{-0.144t}$	−0.963
18.0	19.4	736	8.6	$\ln N_t = 6\,135.52e^{-0.090t}$	−0.993
21.0	28.5	324	6.5	$\ln N_t = 4\,219.17e^{-0.067t}$	−0.996
23.0	33.0	240			
			1981		
10.0	4.7	10 000	25.6	$\ln N_t = 73\,297.62e^{-0.296t}$	−0.980
13.0	9.6	2 355	12.6	$\ln N_t = 10\,274.36e^{-0.112t}$	−0.938
18.0	19.5	621	8.9	$\ln N_t = 7\,898.79e^{-0.093t}$	−0.949
21.0	28.7	263	6.4	$\ln N_t = 3\,414.08e^{-0.066t}$	−0.999
23.0	33.2	195			
			1982		
10.0	4.9	10 000	25.0	$\ln N_t = 93\,821.72e^{-0.287t}$	−0.988
13.0	10.1	2 240	13.2	$\ln N_t = 21\,442.24e^{-0.142t}$	−0.987
18.0	20.6	507	10.8	$\ln N_t = 12\,721.89e^{-0.114t}$	−0.956
21.0	28.4	208	5.9	$\ln N_t = 2\,439.74e^{-0.061t}$	−0.997
23.0	35.7	133			

[a]10 000 larvae at 10 mm was arbitrarily chosen.

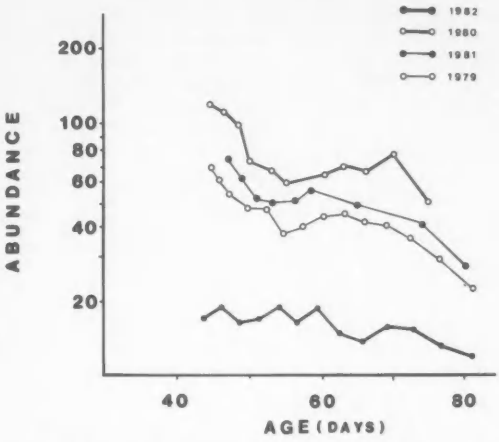

FIG. 5. Survivorship curves for seine-caught shad juveniles between 40 and 80 mm, 1979–82.

no apparent trend with year-class strength. Because mortality rates were consistently higher for first-feeding larvae among the 4 yr, mortality during this 5-d period could greatly affect year-class strength. For example, these mortality estimates indicated that for every 10 000 larvae reaching 4 d old, 176 would have survived to metamorphosis in 1979, 240 in 1980, 195 in 1981, and 133 in 1982.

In each year, the number of juveniles in each age interval declined slowly between 42 and 80 d (Fig. 5). The juvenile mortality estimate for the strong 1980 year-class (1.8%/d) was similar to those of the weak 1982 (1.8%/d) year-class and the moderately weak 1979 (1.9%/d) and 1981 (2.0%/d) year-classes. Despite the relatively high variation in year-class strength from 1979 to 1982, juvenile mortality rates appear to be low and independent of year-class strength.

The strong 1980 year-class was coincident with the highest zooplankton densities during shad larval development (May–July) (Table 5). Zooplankton densities were lowest from May through July 1982, in which the weakest year-class was recorded. Zooplankton densities were intermediate for the moderately weak 1979 and 1981 year-classes. These data suggest that high and persistent zooplankton densities during shad larval development enhance year-class strength of American shad.

TABLE 5. Mean zooplankton density ($\overline{No.}/m^3$) by collection date from 1979 to 1982. Only copepods, cladocerans, and immature insects were tabulated.

Collection date	$\overline{No.}/m^3$	SD	Sample size
	1979		
May 14	278	97	12
May 20	496	168	12
May 27	558	177	12
June 3	532	171	12
June 10	548	194	12
June 17	722	216	12
June 24	1808	806	12
July 1	1899	741	12
July 10	2247	916	12
Mean	1010		
	1980		
May 14	105	38	12
May 20	222	69	12
May 28	1319	293	12
June 3	2822	861	12
June 10	2527	716	12
June 17	2838	883	12
June 24	4187	988	12
July 1	1448	604	12
July 8	939	580	12
July 15	735	414	12
Mean	1714		
	1981		
May 14	411	106	12
May 20	707	188	12
May 27	1040	288	8
June 3	1357	261	8
June 11	1301	247	8
June 17	398	107	8
June 24	349	99	8
July 2	157	50	8
July 7	246	69	8
July 15	236	75	8
Mean	620		
	1982		
May 19	424	123	8
May 26	866	283	8
June 2	803	257	8
June 9	732	259	8
June 16	755	195	8
June 23	520	157	8
June 30	734	206	8
July 7	217	73	8
July 14	172	49	8
Mean	580		

Discussion

Various hypotheses have been offered to explain the causes of erratic fluctuations in year-class strength among fish populations (Hjort 1914; Marr 1956; Nikolskii 1969; May 1974). One of the most controversial is referred to as the "critical period" hypothesis (Hjort 1914), which claims that temporal changes in the abundance of prey organisms influence survival rates of first-feeding larvae and ultimately year-class strength. This hypothesis remains as an appealing explanation for recruitment fluctuations that cannot be ascribed to changes in egg production (May 1974). Gulland (1965) remarked that the "critical period" probably occurs during the larval drift by a combination of biotic and abiotic factors. He also indicated that the hypothesis is supported only if the following criteria are met: (1) that differential mortality occurs prior to the life stage in which year-class strength is established and (2) that the differential mortality rate in question be inversely related to year-class strength, i.e. the mortality rate during the critical period should be highest for an exceptionally weak year-class and lowest for a very strong year-class. As pointed out by Saville (1971), this mortality rate is not required to be the

highest recorded during early development, nor is it necessary that only one critical period occur during prerecruitment.

The survivorship curves for American shad larvae indicate that 70–85% of the losses occur between days 4 and 9 (Fig. 4), thus supporting Hjort's concept of the critical period. These data also support Gulland's two criteria for the critical period hypothesis. Daily mortality rates among American shad larvae were variable and inversely related to year-class strength, while juvenile mortality rates were low and independent of year-class strength. Whether the observed trend in larval mortality and year-class strength is a real phenomenon can only be resolved by correlating larval mortality rates and year-class strength over a number of years. Moreover, estimates of egg mortality are needed annually to determine the degree to which egg mortality rates are related to changes in year-class strength.

There are no published mortality estimates on larval American shad with which these data can be compared. Nevertheless, there have been observations made during shad rearing experiments that corroborate these findings. Bradford et al. (1966) raised American shad larvae in tanks and noted that the highest mortality took place 4–6 d after hatching. Likewise, Mead (1976) and Howey (1981) cultured shad larvae and both reported that mortality levels increased during the initial feeding period (days 3–7).

Gear avoidance by larger and faster swimming larvae was reported to be a serious source of bias in many survivorship studies (May 1974). Since mortality rates of American shad larvae declined with age, gear avoidance by larger larvae does not appear to be a serious source of sampling bias.

Survivorship curves from field surveys are much less consistent than laboratory studies regarding the patterns of age-specific mortality and suffer the criticisms of sampling biases and differing methods of larval growth estimation (May 1974; Dahlberg 1979). Survival rates based on field-caught Pacific herring larvae, *Clupea pallasii* (Stevenson 1962; Iizuka 1966), and Black Sea anchovy, *Engraulis encrasicholus* (Dekhnik 1963), showed no evidence of a critical period after yolk sac absorption. By contrast, survivorship curves for Japanese sardine larvae, *Sardinops melanosticta* (Nakai and Hattori 1962), and Japanese anchovy, *Engraulis japonica* (Nakai et al. 1955), indicated that losses were highest shortly after yolk sac absorption. Similarly, Dragesund and Nakken (1971) reported that 94% of larval Atlantic herring died shortly after feeding commenced, and Schnack (1981) noted a similar mortality rate for first-feeding Pacific herring larvae raised in containers in situ. The mortality rates reported by Dragesund and Nakken (1971) and Schnack (1981) were higher than those presented here for shad larvae between 4 and 8 d old.

The zooplankton densities from 1979 to 1982 (Table 4) suggest that differential larval mortality is due partly to temporal changes in food availability. Short periods of food deprivation among first-feeding larvae could result in death from malnutrition (Blaxter and Ehrlich 1974) because the foraging ability of young herring larvae is greatly limited by their small mouth and poor swimming ability (Lasker 1965; Saksena and Houde 1972). Lack of food would also enhance larval mortality indirectly by reducing larval growth and stamina, thus rendering the larvae vulnerable to predation for prolonged periods (Hempel 1965; Hunter 1976b). Despite the potential linkage between predation-induced mortality and year-class strength, larval predation is a complex process whose interaction with biotic and abiotic factors is difficult to measure in field surveys. It is unreasonable to expect that a single factor alone can explain year-class fluctuations, as other factors such as high and fluctuating flow rates and water temperatures could affect shad larvae directly or indirectly by altering the timing of zooplankton production in the river.

The juvenile indices appear to be useful in detecting very strong (1971) and very weak (1968 and 1973) year-classes but are less useful in predicting moderate year-classes (1967 and 1970). The problem is that the juvenile seine samples a relatively small area and the juvenile spatial and temporal distributions in the river are inherently nonrandom (Marcy 1976), thus affecting the precision and accuracy of the juvenile indices. Another problem is that the qualitative accuracy of the juvenile index cannot be truly assessed until the strength of the respective year-class is measured in the adult population some 4–6 yr later. Also, studies of this type can generate only one pair of data on juvenile relative abundance and larval mortality each year. Therefore, relating larval mortality estimates to juvenile indices and finally to adult recruitment requires a considerable time lag and makes the assessment of the "critical period" hypothesis a very slow process. Despite the inherent limitations associated with relative abundance indices, juvenile surveys of this type represent a valuable "early warning" system with which to predict the extremes in recruitment some 4–5 yr in advance. Hence, potential recruitment failures can be detected early so that management regulations can be imposed on a timely basis.

Growth in length was asymptotic during larval and juvenile development, with one growth stanza evident from hatching to metamorphosis and another through juvenile development. Disjunctive growth patterns have not been documented for young shad in previous studies (Chittenden 1969; Marcy 1976), but seasonal growth stanzas are characteristic of many O group fishes (Pearcy 1962; Beverton 1962; Lockwood 1974; Daan 1975; Sakagawa and Kimura 1976). Other studies on marine herring have demonstrated that larval growth was asymptotic and thus could be represented by a sigmoid growth curve (Kramer and Zweifel 1970; Hunter 1976a; Zweifel and Lasker 1976).

The juvenile mortality rates of American shad are remarkably similar to those of other juvenile fishes. A daily mortality rate of 1.2%/d has been documented for juvenile winter flounder, *Pseudopleuronectes americanus* (Pearcy 1962), 1.7%/d for Atlantic herring (Dragesund 1969), 1.2–2.1%/d for plaice, *Pleuronectes platessa* (Bannister et al. 1974; Lockwood 1981), 2.9%/d for largemouth bass, *Micropterus salmoides* (Timmons et al. 1981), and 1.5%/d for striped bass, *Morone saxatilis* (Dey 1981).

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Estimation of Fish Production Rates and Associated Variances[1]

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NEWMAN, R. M., AND F. B. MARTIN. 1983. Estimation of fish production rates and associated variances. Can. J. Fish. Aquat. Sci. 40: 1729–1736.

Variance estimators for fish production rates are explicitly derived for two production models: the instantaneous growth rate and increment summation methods. Statistics for standing stock, mean interval standing stock, instantaneous growth rate, and production:mean standing stock ($P/\bar{B}$) ratio are presented. The use of a jackknife estimator is proposed for estimating the variance of instantaneous growth rate. Comparison of the results from both production models provides a method of cross-validating results. The use of these statistics is illustrated in example calculations with trout population data. Brook trout (*Salvelinus fontinalis*) annual production in 1969 was significantly higher than combined annual production of brook trout, brown trout (*Salmo trutta*), and rainbow trout (*Salmo gairdneri*) in 1977. Variance estimates are affected by population and mean weight estimates. Validity of the production estimates is based on the validity of model assumptions.

NEWMAN, R. M., AND F. B. MARTIN. 1983. Estimation of fish production rates and associated variances. Can. J. Fish. Aquat. Sci. 40: 1729–1736.

Des estimateurs de variance des taux de production de poisson ont été explicitement dérivés pour deux modèles de production : l'un par la méthode du taux de croissance instantané et l'autre par sommation des accroissements en longueur. Nous présentons des statistiques sur le stock permanent, la moyenne de ce dernier par intervalle, le taux de croissance instantané et le rapport production:stock permanent ($P/\bar{B}$). Pour estimer la variance du taux de croissance instantané, nous proposons l'utilisation d'un estimateur « jackknife ». Comme méthode de vérification des résultats, on peut comparer les deux modèles de production. Pour illustrer la façon dont ces statistiques sont utilisées, nous faisons appel à des données sur des populations de truites. La production annuelle d'omble de fontaine (*Salvelinus fontinalis*) en 1969 a été nettement plus élevée que la production annuelle combinée d'omble de fontaine, de truite brune (*Salmo trutta*) et de truite arc-en-ciel (*Salmo gairdneri*) en 1977. Les estimations de variance sont influencées par celles des populations et des poids moyens. La validité des estimations de production repose sur celle des hypothèses des modèles.

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ESTIMATION of aquatic secondary production has increased greatly in recent years, with concomitant improvements in pertinent methodology. Procedures have been reviewed in several reports (Waters 1977; Gerking 1978; Bagenal 1978). Five basic methods have emerged: (1) increment summation, (2) removal summation, (3) instantaneous growth rate, (4) Allen curve, and (5) size–frequency (Hynes) methods. Most estimates presented for macroinvertebrates have employed the size–frequency method. For fish, the instantaneous growth method has usually been used.

With few exceptions, levels of production have been reported without attempts to compute variances for estimators of production or its component parameters. Several authors have in the past made comparisons of production computed by several methods (e.g. Waters and Crawford 1973; Cushman et al. 1978; Lapchin and Neveu 1980a, b). This procedure is desirable for cross-validation purposes if the data are appropriate. Krueger and Martin (1980) have presented explicit variance estimates for the size–frequency method, and illustrated their use with macroinvertebrate data. Chapman (1967, 1978) presented generalized variance estimators for the instantaneous growth method; however, Chapman's procedures, when applied to field data, are not explicit and require additional assumptions and computations. Waters (1982) used modifications of Chapman's methods to give approximate 95% confidence intervals for brook trout (*Salvelinus fontinalis*) production, but did not provide an explicit description of the computational procedures. Fleeger and Palmer (1982) and Feller (1982) used Chapman's methods to estimate variance of production for meiobenthic copepods and point out the need for the use of production variance estimators.

The purpose of this paper is to provide explicit formulae for the computation of fish production rates and associated

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variances due to sampling for the instantaneous growth rate and increment summation methods. The results from both methods can be compared for field situations, providing a method of cross-validation. This development, based on stream fish populations, assumes that electrofishing is the primary sampling method. With some modifications, the computational methods are applicable to aquatic macroinvertebrate populations.

The instantaneous growth rate model computes production as the product of the instantaneous growth rate (G) and mean biomass ($\bar{B}$) for a time interval (int), of time t to $t+1$, where

$$(1) \quad G_{int} = \log_e \bar{w}_{t+1} - \log_e \bar{w}_t$$

$$(2) \quad \bar{B}_{int} = (B_t + B_{t+1})/2$$

where $\bar{w}_t$ is the mean individual weight. Equation 1 assumes exponential growth over the interval. Equation 2 assumes a linear change in biomass. For simplicity in variance estimation and reasons discussed by Chapman (1978, p. 208), Ricker's exponential standing stock equation (see Waters 1977; Chapman 1978) will not be used.

The discrete increment summation production model is defined as

$$P_{(\text{inc. sum.})_{int}} = \bar{N}_{int}\,\Delta\bar{w}$$

(see Waters 1977; Gillespie and Benke 1979), where $\bar{N}_{int}$ is the mean number over time, of individuals in the interval and $\Delta\bar{w}$ is the change in mean weight. This model assumes a linear change in numbers (mortality) and growth (in weight). The method is arithmetically identical to the removal summation method (Gillespie and Benke 1979), and the computations can be made over an interval for any identifiable cohort. In a computer simulation, Cushman et al. (1978) modeled aquatic insect populations, and determined that the removal summation method was more accurate, as well as more robust to model assumption violations, than the instantaneous growth method.

Notation

Sampling dates are indexed by i ($i = 1,2,\ldots,a$) for a total sampling dates. Age of a given cohort is indexed by j ($j = 1,2,\ldots,b$), b being the oldest cohort. Size (in length) is indexed by k ($k = 1,2,\ldots,c$), c being the largest length group. Because of known size biases in electrofishing sampling, computations are done by length groups in each age class (see Lagler 1978; Waters 1982). Individual observations are indexed by l ($l = 1,2,\ldots,m_{ijk}$), m_{ijk} being the total number of observations in the appropriate cell. Intervals between sample dates are indexed by int ($int = 1,2,\ldots,f$), with f being the last interval, ending at sample date a.

Methods

At each of the i sampling dates, a single census Petersen mark–recapture population estimate (Youngs and Robson 1978) is made. The date of the marking run is defined as the ith date. The date of the sampling run will be considered the same as the marking run. All fish handled are measured for length, and marks made or noted. In each length class caught, subsamples of arbitrary size $m_{i\cdot k}$ of fish are precisely measured, weighed, and aged. If the investigator so wishes, $m_{i\cdot k}$ could be the size of the entire catch of length k. Fish are aged by the appropriate method, and age, weight, and length data tabulated.

Population Estimation

From the field data, the numbers of marked, captured and recaptured fish are obtained as

$M_{i\cdot k}$ = the number of marked fish of length group k in the population on date i
$C_{i\cdot k}$ = total number of fish of length group k, on date i captured on the sample run
$R_{i\cdot k}$ = the number of M recaptured on the sample run.

If the assumptions of the Petersen single-census mark–recapture method (Youngs and Robson 1978) are met (see Heggberget and Hesthagen 1979 for a discussion of assumption violations), the population size of length group k on date i is estimated as

$$(3a) \quad \hat{N}_{i\cdot k} = \frac{M_{i\cdot k}\,C_{i\cdot k}}{R_{i\cdot k}}$$

with estimated variance

$$(3b) \quad V(\hat{N}_{i\cdot k}) = \frac{\hat{N}^2_{i\cdot k}(\hat{N}_{i\cdot k} - M_{i\cdot k})\,(\hat{N}_{i\cdot k} - C_{i\cdot k})}{(\hat{N}_{i\cdot k} - 1)\,M_{i\cdot k}C_{i\cdot k}}$$

assuming sampling is without replacement (see Youngs and Robson 1978).

If each individual fish handled is aged correctly, the proportion of each length group (k) that is a particular age (j), is

$$\hat{p}_{ijk} = \frac{m_{ijk}}{m_{i\cdot k}}$$

where $m_{i\cdot k}$ is the arbitrarily chosen number of fish of a given length group k that were weighed and aged and m_{ijk} is the number of these fish which were found to be of age j. Aging is assumed to be correctly done, but this assumption may not be critical since errors in age determination may not have a major effect on production estimates (Le Cren 1974), relative to other sources of error.

Sampling error of $\hat{p}_{ijk}$ may be determined as

$$V(\hat{p}_{ijk}) = \frac{(1 - \hat{p}_{ijk})\,\hat{p}_{ijk}}{m_{i\cdot k}}.$$

The covariance between proportions for different ages in the same length class is

$$\text{Cov}(\hat{p}_{ijk}, \hat{p}_{ij'k}) = -\frac{\hat{p}_{ijk}\,\hat{p}_{ij'k}}{m_{i\cdot k}}$$

and is negative.

Estimates of population sizes may be computed for each age-class using the $\hat{p}_{ijk}$'s, as follows

$$(4a)\quad \hat{N}_{ij\cdot} = \sum_{k=1}^{c} \hat{p}_{ijk}\hat{N}_{i\cdot k} = \sum_{k=1}^{c} \hat{N}_{ijk}$$

where

$$\hat{N}_{ijk} = \hat{p}_{ijk}\hat{N}_{i\cdot k}.$$

The variance of this population estimate for age j can be estimated by

$$(4b)\quad V(\hat{N}_{ij\cdot}) = \sum_{k=1}^{c} V(\hat{N}_{ijk}) = \sum_{k=1}^{c} [\hat{p}_{ijk}^2\, V(\hat{N}_{i\cdot k}) + \hat{N}_{i\cdot k}^2\, V(\hat{p}_{ijk})].$$

An expression for the covariance of estimates of population abundance of any two age-classes is

$$\mathrm{Cov}\,(\hat{N}_{ij\cdot}, \hat{N}_{ij'\cdot}) = \sum_{k=1}^{c} \left[\hat{p}_{ijk}\,\hat{p}_{ij'k}\left(V\,(\hat{N}_{i\cdot k}) - \frac{\hat{N}_{i\cdot k}^2}{m_{i\cdot k}}\right)\right].$$

For many practical field sampling situations, the negative terms in the above covariance will be predominant and the covariance would be negative (i.e. $V(\hat{N}_{i\cdot k})$ will be smaller than $\hat{N}_{i\cdot k}^2/m_{i\cdot k}$, since with low R/C ratios, $m_{i\cdot k}$ will be a small proportion of $\hat{N}$ and with high R/C ratios, $V(\hat{N})$ will be small).

Weight Estimation

Since R/C ratios will vary with size when sampling via electrofishing (see Lagler 1978), the unweighted mean estimator of average age-group weight (equation 5) will likely produce biased results.

$$(5)\quad \bar{w}_{ij\cdot} = \frac{\sum_{k=1}^{c}\left(\sum_{l=1}^{m_{ijk}} w_{ijkl}\right)}{m_{ij\cdot}}$$

If we restrict out attention however, to any given narrow length strata (group) of an age or cohort (e.g. 2 cm for salmonids), catchability will be effectively constant and mean weight and variance of a length strata can be computed as

$$(6a)\quad \bar{w}_{ijk} = \frac{\sum_{l=1}^{m_{ijk}} w_{ijkl}}{m_{ijk}}$$

with

$$(6b)\quad V(\bar{w}_{ijk}) = \frac{\sum_{l=1}^{m_{ijk}} (w_{ijkl} - \bar{w}_{ijk})^2}{m_{ijk}\,(m_{ijk} - 1)}$$

which is the simple variance estimate of the mean of a sample of m_{ijk} observations. The mean weight of a given age ($\bar{w}_{ij\cdot}$) can then be determined as the "weighted" (by $\hat{N}_{ijk}$) average of the length strata mean weights.

$$(7a)\quad \bar{w}_{ij\cdot} = \frac{\sum_{k=1}^{c} \hat{N}_{ijk}\,(\bar{w}_{ijk\cdot})}{\sum_{k=1}^{c} \hat{N}_{ijk}}$$

with approximate variance estimated by

$$(7b)\quad V(\bar{w}_{ij\cdot}) = \frac{\sum_{k=1}^{c} \hat{N}_{ijk}^2\, V(\bar{w}_{ijk})}{\hat{N}_{ij\cdot}^2} + \frac{\sum_{k=1}^{c} (\bar{w}_{ijk} - \bar{w}_{ij\cdot})^2\, V(\hat{N}_{ijk})}{\hat{N}_{ij\cdot}^2}.$$

If the investigator wishes to make this estimate conditional on $\hat{N}_{ijk}$, the second term in the equation may be dropped resulting in

$$(7c)\quad V(\bar{w}_{ij\cdot}) = \frac{\sum_{k=1}^{c} \hat{N}_{ijk}^{\,2}\, V(\bar{w}_{ijk\cdot})}{\left(\sum_{k=1}^{c} \hat{N}_{ijk}\right)^2}.$$

In this case, estimating the precision of mean weights for the population will be considered independent of the "weighting" factor ($\hat{N}_{ijk}$).

Standing Stock Estimation

Biomass B for time i, age j, is estimated as the product of the estimated population ($\hat{N}_{ij}$) and the mean individual weight ($\bar{w}_{ij\cdot}$),

$$(8)\quad \hat{B}_{ij\cdot} = \hat{N}_{ij\cdot}\,(\bar{w}_{ij\cdot}) = \sum_{k=1}^{c} \hat{p}_{ijk}\,\hat{N}_{i\cdot k}\,\bar{w}_{ijk}.$$

Since, $\hat{N}_{i\cdot k}$ and $\bar{w}_{ijk}$ are statistically independent estimates, variance of $\hat{B}_{ij\cdot}$ can be estimated by,

$$(8b)\quad V(\hat{B}_{ij\cdot}) = \sum_{k=1}^{c} [\hat{p}_{ijk}^2\,\hat{N}_{i\cdot k}^2\, V(\bar{w}_{ijk}) + \bar{w}_{ijk}^2\, V(\hat{N}_{ijk})]$$

where $V(\hat{N}_{ijk})$ is given in equation (4b). Chapman (1967, 1978) included a cov $(\hat{N}_{ij\cdot}, \bar{w}_{ij\cdot})$ term, which would be

negative due to biological density dependence, a population parameter. Since we are considering only sampling error, our inference is intended for the static state at the time of sampling and not for a dynamic population process.

Interval Standing Stock Estimation

Using the linear change in biomass model (equation 2), mean sampling interval standing stock, $\bar{B}_{intj}$ for age j is estimated as

$$(9a)\quad \hat{\bar{B}}_{intj} = \frac{\hat{B}_{ij} + \hat{B}_{i+1,j}}{2}.$$

Sampling variance of mean interval standing stock $\hat{\bar{B}}_{intj}$ is computed as

$$(9b)\quad V(\hat{\bar{B}}_{intj}) = \frac{1}{4}\left[V(\hat{B}_{ij}) + V(\hat{B}_{i+1,j})\right]$$

since the sampling error for $\hat{B}_{ij}$ estimation is independent for separate sampling dates.

Total standing stock for a given date can be computed by summing $\hat{B}_{ij}$ for all j. Total standing stock for an interval can be computed by summing the $\bar{B}_{intj}$ for all j. However, calculation of the variances of either $\hat{B}_{i\cdot}$ or $\bar{B}_{int\cdot}$ is complicated by the covariance of the estimates of standing stock of different ages on the same date.

For example,

$$V(\hat{B}_{i\cdot}) = \sum_{j=1}^{b} V(\hat{B}_{ij}) + \sum_{j\neq j'}^{b} \operatorname{cov}(\hat{B}_{ij}, \hat{B}_{ij'}).$$

Since the $\hat{N}_{ij}$'s were estimated using estimated p_{ijk}'s, then

$$(10)\quad \operatorname{cov}(\hat{B}_{ij}, \hat{B}_{ij'}) = \sum_{k=1}^{c}\left[\hat{p}_{ijk}\,\hat{p}_{ij'k}\,\bar{w}_{ijk}\,\bar{w}_{ij'k}\left(V(\hat{N}_{i\cdot k}) - \frac{\hat{N}^2_{i\cdot k}}{m_{ijk}}\right)\right].$$

Since an overestimate of the biomass of a given age will result in an underestimate of the biomass of the adjacent ages (due to the covariance of the $\hat{p}_{ijk}$'s) this covariance will generally be negative. The estimate of this covariance will be negative for most field data (see rationale for the cov $(\hat{N}_{ij}, \hat{N}_{ij'})$) and simply summing the variances should provide a conservative estimate of total variance.

$$(11)\quad V(\hat{B}_{i\cdot}) = \sum_{j=1}^{b} V(\hat{B}_{ij})$$

Instantaneous Growth Estimation

Instantaneous growth rate for a cohort over an interval is computed as

$$(12)\quad G_{intj} = \log_e \frac{\bar{w}_{i+1,j}}{\bar{w}_{ij}} = \log_e \bar{w}_{i+1,j} - \log_e \bar{w}_{ij}.$$

Chapman (1967, 1978) suggests several subset estimates of G could be used to estimate the variance of G as

$$(13)\quad V(G_{intj}) = \frac{\sum_{l=1}^{m_{int\,j}} (G_{int\,j\,l} - \bar{G}_{int\,j\cdot})^2}{(m_{int\,j} - 1)}.$$

Equation 13 requires the identification of individual fish over the interval or some method of randomly obtaining several $\bar{w}_{ij}$'s. Identification of substantial numbers of individual fish is often not feasible in production estimates and adds another degree of complexity (marking effects, losses of marks and marked fish, etc. . . .).

Variance of G is also the pooled variance of the difference between the natural logarithms of two mean weights,

$$V(G_{intj}) = V(\log_e \bar{w}_{i+1,j} - \log_e \bar{w}_{ij}).$$

If catchability bias due to size can be ignored (as in equation 5), an approximately unbiased, distribution free, estimate of $\log_e \bar{w}$ and its variance can be obtained via jackknifing (Mosteller and Tukey 1977 Chapter 8). The method uses the effect of repeated calculation of the estimate while leaving each individual observation in turn, out of the data set. In this manner, a set of m_{ijk} different "estimates" is defined. Following the notation and terminology of Mosteller and Tukey (1977), define:

$$\log_e(\bar{w}_{ij\cdot})_{(L)} = \log_e\left[\frac{\sum_{l\neq L}^{m_{ij\cdot}-1} w_{ij\cdot l}}{m_{ij\cdot} - 1}\right],$$

with the Lth observation left out ($L = 1,2,\ldots m_{ij\cdot}$). A set of $m_{ij\cdot}$ pseudo-values for $\log_e(\bar{w})$ is defined by:

$$\log_e(\bar{w}_{ij\cdot})_{*(L)} = m_{ij\cdot}\log_e(\bar{w}_{ij\cdot}) - (m_{ij\cdot} - 1)\log_e(\bar{w}_{ij\cdot})_{(L)}.$$

The jackknifed logarithm of the mean weight is

$$(14)\quad \log_e(\bar{w}_{ij\cdot})_* = \frac{\sum_{L=1}^{m_{ij\cdot}} (\log_e \bar{w}_{ij\cdot})_{*(L)}}{m_{ij\cdot}}$$

which is the simple average of the pseudo-values and its variance is estimated by

$$(15)\quad V(\log_e \bar{w}_{ij})_* = \frac{1}{m_{ij}} V(\log_e \bar{w}_{ij\cdot})_*$$

$$= \frac{1}{m_{ij}} \frac{\sum_{L=1}^{m_{ij}} [(\log_e \bar{w}_{ij})_{*L} - \log_e \bar{w}_{ij\cdot})_*]^2}{m_{ij} - 1}.$$

Instantaneous growth rate is computed as

$$(16)\quad \hat{G}_{intj} = (\log_e \bar{w}_{i+1,j})_* - (\log_e \bar{w}_{ij})_*.$$

The variance can be estimated as

$$(17)\quad V(\hat{G}_{int\cdot}) = V(\log_e \bar{w}_{ij})_{\cdot} + V(\log_e \bar{w}_{i+1,j})_{\cdot}$$

since the $\log_e (\bar{w}_{ij})_{\cdot}$'s are statistically independent.

When, as noted for equation 5, the mean weight $\bar{w}_{ij\cdot}$ may be biased (due to electrofishing) for age j, the above jackknife estimates must be computed for each length group ($\log_e (\bar{w}_{ijk})_{\cdot}$) and "weighted" by the proportion of each length group that is age j using "weights" given by $\frac{\hat{N}_{ijk}}{\hat{N}_{ij\cdot}}$. The "weighting" is accomplished in a similar manner to the mean weight estimation in equations 7a and b.

Instantaneous Growth Rate Production Estimates

Production is computed by the instantaneous growth method for an interval as

$$(18)\quad \hat{P}_{intj} = \hat{\bar{B}}_{intj}\,\hat{G}_{intj}$$

with approximate variance (see Goodman 1960; Chapman 1967)

$$V(\hat{P}_{intj}) = V(\hat{\bar{B}}_{intj})\hat{G}_{intj}^{\,2} + \hat{\bar{B}}_{intj}^{\,2}\,V(\hat{G}_{intj}) + 2\hat{G}_{intj}\,(\hat{\bar{B}}_{intj})\,\mathrm{cov}\,(\hat{G}_{intj}, \hat{\bar{B}}_{intj}).$$

Sampling errors in $\hat{\bar{B}}_{intj}$ and $\hat{G}_{intj}$ will not be independent since each will have $\bar{w}_i$ and $\bar{w}_{i+1}$ in common. Overestimation of $\bar{B}_{intj}$ may be associated with either an under or overestimate of G_{intj}, depending on whether it is $\bar{w}_{ij}$ or $\bar{w}_{i+1,j}$ that has the larger positive sampling deviation. The same is true for underestimation of $\bar{B}_{intj}$. Since the sampling errors in the $\bar{w}_{ij}$'s and $\bar{w}_{i+1,j}$'s are independent from i to $i+1$, then in expectation there will be a balancing out of the over and underestimation for any value of $\bar{B}_{intj}$. Thus, we expect the covariance to be near zero and variance can be reasonably safely estimated by dropping the covariance term, resulting in

$$(19)\quad V(\hat{P}_{intj}) = V(\hat{\bar{B}}_{intj})\hat{G}_{intj}^{\,2} + \hat{\bar{B}}_{intj}^{\,2}\,V(\hat{G}_{intj}).$$

Within an interval i to $i+1$, the production estimates of each age-class or cohort will be uncorrelated if the $\bar{B}_{intj}$'s are uncorrelated. This will not be the case if the p_{ijk}'s are estimated, as in equation 10. In calculating the variance of total interval production the covariance terms can be omitted, using the same rationale for omitting the term expressed in equation 10, and simply summing the variances should result in a conservative estimate of variance. Total interval production and its variance can be computed by summing the respective estimates.

$$\hat{P}_{int\cdot} = \sum_{j=1}^{b} \hat{P}_{intj}$$

$$V(\hat{P}_{int\cdot}) = \sum_{j=1}^{b} V(\hat{P}_{intj}).$$

If production estimates for adjacent intervals can be assumed either independent or negatively correlated, production over several intervals (e.g. annual production) can be computed as

$$\hat{P}_{\cdot\cdot} = \sum_{int=1}^{f} \hat{P}_{int\cdot}$$

with estimated variance

$$V(\hat{P}_{\cdot\cdot}) = \sum_{int=1}^{f} V(\hat{P}_{int\cdot}).$$

If the estimates are not independent and are positively correlated, the variance may be estimated as

$$V(\hat{P}_{\cdot\cdot}) = \sum_{int=1}^{f} V(\hat{P}_{int\cdot}) + 2(\text{all pairwise covariance terms}).$$

Approximate 95% confidence intervals, representing ±2 SE's for all estimates may be obtained as two times the square root of the variance.

Increment Summation Production Estimation

Increment summation production is estimated discretely as

$$(20)\quad \hat{P}_{intj} = \hat{\bar{N}}_{intj}\,\Delta\bar{w}_{intj}$$

(see Gillespie and Benke 1978), where:

$$(21)\quad \hat{\bar{N}}_{intj} = \frac{\hat{\bar{N}}_{ij} + \hat{\bar{N}}_{i+1,j}}{2}$$

$$(22)\quad \Delta\bar{w}_{intj} = \bar{w}_{i+1,j} - \bar{w}_{ij}.$$

The population estimates at time i and $i+1$ are statistically independent and $V(\bar{N}_{int\,j})$ is estimated as

$$(23)\quad V(\hat{\bar{N}}_{intj}) = \frac{1}{4}\left[V(\hat{N}_{ij}) + V(\hat{N}_{i+1,j})\right].$$

The variance of the difference in mean weights is computed, using equation 6b or 7b, as

$$(24)\quad V(\Delta\bar{w}_{intj}) = V(\bar{w}_{i+1,j}) + V(\bar{w}_{ij}).$$

Mean numbers ($\hat{\bar{N}}_{intj}$) and mean weight ($\bar{w}_{ij}$) have statistically independent sampling distributions. The sampling variance of production can be estimated as

$$(25)\quad V(\hat{P}_{intj}) = \hat{\bar{N}}_{intj}^{\,2}\,V(\Delta\bar{w}_{intj}) + \Delta\bar{w}_{intj}^{\,2}\,V(\hat{\bar{N}}_{intj}).$$

Mean Standing Stock and $P/\bar{B}$ Estimation

Mean biomass or standing stock over two or more sample dates (e.g. mean annual standing stock) can be estimated by

TABLE 1. Instantaneous growth and increment summation production rate computations with variances for rainbow trout, Valley Creek, MN, April 1977–April 1978.

	Instantaneous growth rate production							Increment summation production						
	April 1977–Sept. 1977			Sept. 1977–April 1978				April 1977–Sept. 1977			Sept. 1977–April 1978			
Year-class	B_{1j}, kg/ha	G_{1j}	P_{1j}, kg/ha	B_{2j}, kg/ha	G_{2j}	P_{2j}, kg/ha	$P_{\cdot j}$, kg/ha	N_{1j}, N/ha	Δw_{1j}, g	P_{1j}, kg/ha	N_{2j}, N/ha	Δw_{2j}, g	P_{2j}, kg/ha	$P_{\cdot j}$, kg/ha
1977	0.0	0.0	4.396	6.688	1.0457	6.994	11.390	0.0	0.0	4.396	785.6	9.3	7.314	11.710
Variance	0.0	0.0	0.249	0.464	0.0222	1.499	1.748	0.0	0.0	0.379	6977.7	1.7	1.647	2.027
1976	10.226	1.0837	11.081	13.128	0.4233	5.557	16.638	348.7	36.0	12.544	192.4	27.1	5.215	17.759
Variance	3.627	0.0195	6.294	3.430	0.0165	3.451	9.746	1659.1	70.9	10.125	376.9	88.6	3.557	13.682
1975	7.453	0.3015	2.247	7.731	0.4256	3.291	5.538	68.2	45.4	3.097	47.2	52.2	2.463	5.560
Variance	4.199	0.3015	9.547	3.549	0.1686	10.718	20.265	324.6	905.0	4.882	207.6	1233.6	3.315	8.197
1974	13.352	0.4123	5.504	0.0	0.0	0.0	5.504	74.9	82.4	6.172	0.0	0.0	0.0	6.172
Variance	24.791	0.0168	6.118	0.0	0.0	0.0	6.118	763.5	670.9	8.949	0.0	0.0	0.0	8.949
Total $P_{i\cdot}$			23.228			15.842	39.070			26.209			14.992	41.201
Variance			22.208			15.668	37.877			24.335			8.519	32.855

TABLE 2. Instantaneous growth and increment summation production rate computations with variances for brown trout, Valley Creek, MN, April 1977–April 1978.

	Instantaneous growth rate production							Increment summation production						
	April 1977–Sept. 1977			Sept. 1977–April 1978				April 1977–Sept. 1977			Sept. 1977–April 1978			
Year-class	B_{1j}, kg/ha	G_{1j}	P_{1j}, kg/ha	B_{2j}, kg/ha	G_{2j}	P_{2j}, kg/ha	$P_{\cdot j}$, kg/ha	N_{1j}, N/ha	Δw_{1j}, g	P_{1j}, kg/ha	N_{2j}, N/ha	Δw_{2j}, g	P_{2j}, kg/ha	$P_{\cdot j}$, kg/ha
1977	0.0	0.0	7.504	9.258	0.8881	8.222	15.726	0.0	0.0	7.504	1073.4	7.9	8.452	15.956
Variance	0.0	0.0	0.444	0.289	0.0117	1.229	1.673	0.0	0.0	0.654	3344.3	0.6	0.942	1.597
1976	6.190	1.0623	6.576	8.291	0.4675	3.876	10.452	287.2	23.5	6.752	166.5	35.7	5.936	12.688
Variance	0.188	0.0074	0.498	0.925	0.0246	1.890	2.388	519.8	4.0	0.620	197.9	61.0	1.943	2.562
1975	8.663	0.5263	4.559	11.530	0.2513	2.897	7.457	88.4	52.6	4.646	79.9	42.5	3.398	8.043
Variance	1.146	0.0074	0.873	2.065	0.0139	1.980	2.854	94.3	79.0	0.878	90.2	340.9	2.339	3.216
1974	9.371	0.4791	4.490	8.782	0.0634	0.556	5.046	40.5	97.2	3.939	27.6	26.5	0.732	4.671
Variance	0.424	0.0097	0.950	0.882	0.0056	0.438	1.388	27.1	289.3	0.731	10.8	1664.1	1.278	2.009
Total $P_{i\cdot}$			23.129			15.551	38.680			22.840			18.517	41.357
Variance			2.765			5.537	8.303			2.883			6.502	9.384

$$(26)\quad \bar{B}_{\cdot\cdot} = \frac{\sum_{i=1}^{a-1} (D_{i+1} - D_i)\dfrac{\hat{B}_{i\cdot} + \hat{B}_{i+1\cdot}}{2}}{D_a - D_1}$$

where D is the number of days between the first sample date and the ith sample date. The variance is estimated as

$$(27)\quad V(\hat{\bar{B}}_{\cdot\cdot}) = \left\{(D_2 - D_1)^2\left[\frac{V(\hat{B}_1)}{4}\right] + \sum_{i=2}^{a-1}(D_{i+1} - D_{i-1})^2\left[\frac{V(\hat{B}_i)}{4}\right] + (D_a - D_{a-1})^2\left[\frac{V(\hat{B}_a)}{4}\right]\right\}\Big/(D_a - D_1)^2$$

since biomass estimates at each date are based on statistically independent population and mean weight estimates.

The ratio of production to mean biomass ($P/\bar{B}$) is often a parameter of interest (Waters 1977). Assuming the means and variances of production and biomass are unbiased estimators of their expected values, variance of $P/\bar{B}$ can be estimated as

$$(28)\quad V(\hat{P}_{\cdot}/\hat{\bar{B}}_{\cdot}) = \frac{\hat{P}_{\cdot}^2}{\hat{\bar{B}}_{\cdot}^2}\left[\frac{V(\hat{P}_{\cdot})}{\hat{P}_{\cdot}^2} + \frac{V(\hat{\bar{B}}_{\cdot})}{\hat{\bar{B}}_{\cdot}^2} - \frac{2\mathrm{cov}\,(\hat{P}_{\cdot},\hat{\bar{B}}_{\cdot})}{\hat{P}_{\cdot}\,\hat{\bar{B}}_{\cdot}}\right]$$

(see Kendall and Stuart 1969, p. 232). Production is expected to be positively correlated with $\bar{B}$ (Waters 1977), and the covariance term can be dropped providing a conservative estimate of variance.

Application

Using several FORTRAN77 programs (available, with documentation, from R. M. Newman), production estimates were computed using the preceding equations, for data from Valley Creek, Minnesota (T. F. Waters, unpublished data). Production was computed for brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and rainbow trout (*Salmo gairdneri*) for April 1977 to April 1978. Population estimates and age, length, and weight data were obtained in April 1977, September 1977, and April 1978 (see Waters 1982, for methods). The results for rainbow trout and brown trout are presented in Tables 1 and 2. Note that the production estimate and associated variance for the newly recruited 1977 year group in September 1977 is the standing stock estimate and its variance. Since the 1977 year-class was not sampled in the spring, no interval standing stock or growth rate was computed for the first interval. For intervals with negative growth, production, and its variance were assumed to be zero (see Waters 1977; Chapman 1978). Variances for the estimates can be converted to approximate 95% confidence intervals by multiplying the square root of the variance by two.

Annual production estimates for all three species overlap at the 95% confidence level (Tables 1 and 2; brook trout production = 46.1 $kg \cdot ha^{-1} \cdot yr \pm 8.7$ for instantaneous growth; 47.9 $kg \cdot ha^{-1} \cdot yr \pm 9.2$ for increment summation). The close agreement of the increment summation and instantaneous growth estimates suggests that the data presented are not sensitive to the differences in assumptions of the two models. Statistically significant differences between methods would have indicated possible assumption violations. Production estimates by increment summation for each species were somewhat higher than those obtained from instantaneous growth, a finding supported by Cushman et al. (1978) and the models presented here.

Differences in population parameters can be examined using component estimates such as mean standing stock and instantaneous growth rate. For example, production of 1976 year-class rainbow trout was notably higher than 1976 year-class brown trout during the April to September interval (rainbow trout $P = 11.1\ kg \cdot ha^{-1} \cdot yr \pm 5.0$; brown trout $P = 6.6\ kg \cdot ha^{-1} \cdot yr \pm 1.4$). This difference in production is likely not due to the instantaneous growth rate (rainbow trout $G = 1.08 \pm 0.28$; brown trout $G = 1.06 \pm 0.17$), but rather, the higher mean standing stock of rainbow trout (rainbow trout $B = 10.2\ kg \cdot ha^{-1} \pm 3.8$; brown trout $B = 6.2\ kg \cdot ha^{-1} \pm 0.9$).

Annual production was also computed for brook trout in Valley Creek, 1969–70 using the same methods. Brown and rainbow trout populations were too low to provide reliable variance estimates. Brook trout production was estimated at 177.8 $kg \cdot ha^{-1} \cdot yr \pm 20.9$ for instantaneous growth and 179.0 $kg \cdot ha^{-1} \cdot yr \pm 18.9$ for increment summation. These estimates indicate a significantly higher brook trout production in 1969–70 than production of the three species combined in 1977–78 (total production = 123.8 $kg \cdot ha^{-1} \cdot yr \pm 16.2$ for instantaneous growth; 130.4 $kg \cdot ha^{-1} \cdot yr \pm 15.9$ for increment summation).

The variance of estimates of standing stock, growth rate and production rate are affected by the variance in the estimation of population abundance and mean weight for a cohort. High R/C ratios within age-classes will provide population estimates with low variance. In small streams violation of the assumption of random sampling may not be appreciable, but additional recapture samples may be used to validate population estimate assumptions. Precise individual weight determination and adequate sample size within a cohort will provide low variances for mean weight and instantaneous growth rate. The lower variance of production of brown trout in 1977 than rainbow trout was due to higher R/C ratios and lower variation in individual weights. As previously noted, most violations of model assumptions may not be accounted for in the statistics. Since the increment summation and instantaneous growth methods, as considered, are cohort based, and annual estimates are based on the summation of estimates, little or no gain in statistical precision will be realized by increasing the number of sample dates. The size–frequency method, which is not cohort based, realizes an increase in precision with more sample dates (which effectively increases sample size) (see Krueger and Martin 1980). Realistic numbers of intervals need to be sampled based on the age structure of the population. The computation of variance will provide an estimate of the precision of the statistics, and allow comparisons of various estimates.

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Mercury Levels in the Sunfish, *Lepomis gibbosus*, Relative to pH and Other Environmental Variables of Precambrian Shield Lakes

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WREN, C. D., AND H. R. MACCRIMMON. 1983. Mercury levels in the sunfish, *Lepomis gibbosus*, relative to pH and other environmental variables of Precambrian Shield lakes. Can. J. Fish. Aquat. Sci. 40: 1737–1744.

Growth rate and total mercury concentrations were determined in muscle tissue of pumpkinseed sunfish (*Lepomis gibbosus*) collected from 16 waters in south-central Ontario. Mean water pH ranged from 5.6 to 8.4. Growth rate is correlated positively with lake pH, whereas fish mercury levels are higher at lower pH. Differences in growth rate may be the result of both metal and acid stress in the lower pH waters. Pumpkinseed mercury levels can be accurately described by an equation incorporating chemical and physical lake variables.

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Le taux de croissance et les concentrations de mercure total ont été déterminés dans le tissu musculaire de crapets soleils (*Lepomis gibbosus*) recueillis dans 16 eaux du centre-sud de l'Ontario. Le pH moyen de l'eau variait de 5,6 à 8,4. On observe une corrélation positive entre le taux de croissance et le pH, tandis que les niveaux de mercure dans les poissons sont plus élevés à de bas pH. Il se peut que les différences de taux de croissance résultent du stress causé à la fois par les métaux et l'acide dans les eaux de bas pH. On peut décrire avec précision à l'aide d'une équation incorporant les variables chimiques et physiques des lacs les niveaux de mercure dans les crapets soleils.

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EVENTS leading to general concern about Hg contamination in the environment are well documented (i.e. D'Itri and D'Itri 1977). Of more recent interest are findings of high Hg levels in fish from lakes remote from any direct source of contamination, especially those of the Canadian Precambrian Shield (Fimreite and Reynolds 1973; Smith and Berkes 1975; Ontario Ministry of the Environment 1977; MacCrimmon et al. 1983). Natural Hg deposits are known to occur in some areas of bedrock mineralization near the latter waters (Allan et al. 1974), but these occurrences do not sufficiently explain the often substantial differences in fish Hg levels observed between lakes situated close to each other.

It has now been established that in addition to the concentration of Hg in the water and diet of a fish, the uptake of Hg by fish is influenced by several biotic and abiotic factors, including fish growth and metabolic rate (Olsson 1976; Norstrom et al. 1976; Rodgers and Beamish 1981), fish body size (de Freitas and Hart 1975; Sharpe et al. 1977), water temperature (MacLeod and Pessah 1973; Reinert et al. 1974), calcium (McFarlane and Franzin 1980), alkalinity (Kleinert and Degurse 1972; Schneider et al. 1979), hardness (Rodgers 1982), and pH (Jernelov et al. 1975; Suns et al. 1980; Hakanson 1980). It has been shown, also, that fish Hg levels may be related to lake morphometric parameters such as the ratio of drainage area to lake volume (Suns et al. 1980). However, in natural lake ecosystems, it is difficult to isolate the relative influences of individual environmental conditions on observed fish Hg levels because of known correlations between several morphometric and limnological variables (Ryder 1965; Schindler 1971; Conroy and Keller 1976).

Given that, either directly or indirectly, acid precipitation can alter the bioavailability of metals in aquatic ecosystems, it is imperative to identify those lakes in which there is increased uptake of toxic metals, such as Hg, by fish. The present study was undertaken to explore more fully the relationships between fish Hg levels and ambient environmental conditions in a series of nonstressed and acid-stressed waters in Ontario using the pumpkinseed sunfish, *Lepomis gibbosus*, as the test species.

Materials and Methods

STUDY AREA

Pumpkinseed sunfish were collected from a total of 16 waters in south-central Ontario (Table 1). Twelve of the waters are headwater lakes situated on the Grenville structural province of the Canadian Precambrian Shield characterized by granite rock, generally granite–gneisses (Chapman 1975), which provides very low buffering capacity to the surface

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TABLE 1. Water bodies sampled in 1981.

Lake	Township	County	Latitude	Longitude
Basshaunt	Guilford	Haliburton	45°47′	78°28′
Bigwind	Oakley	Muskoka	45°03′	79°03′
Crosson	Oakley	Muskoka	45°05′	79°02′
Dickie	McLean	Muskoka	45°09′	79°05′
Farlain	Tiny	Simcoe	44°49′	79°59′
Fawn	Macauley	Muskoka	45°10′	79°15′
Georgian Bay	—	—	—	—
Greenbass	Freeman	Muskoka	45°04′	79°57′
Healey	Macauley	Muskoka	45°05′	79°11′
Heney	McLean	Muskoka	45°08′	79°06′
Leech	Oakley	Muskoka	45°03′	79°06′
Leonard	Monck	Muskoka	45°04′	79°27′
Plastic	Sherborne	Muskoka	45°11′	78°50′
Tadenac Bay	Freeman	Muskoka	45°04′	79°58′
Tadenac	Freeman	Muskoka	45°04′	79°57′
Walker	Sinclair	Muskoka	45°22′	79°04′

TABLE 2. Water chemistry of study lakes. Each reported value represents the mean of measurements from epilimnion, metalimnion, and hypolimnion and for a minimum of six different times throughout the year. Mean pH value was obtained by calculating the logarithm of the average hydrogen ion concentration of repeated observations.

Lake	pH	Conductivity (μmhos/cm)	Alkalinity (mg/L)	Ca (mg/L)	Fe (mg/L)	Total P (μg/L)	Total Kjeldahl N (μg/L)	Secchi disc (m)
Basshaunt	6.6	45.2	9.3	4.4	0.08	7.6	259	4.9
Bigwind	6.2	31.6	5.8	3.0	0.11	7.8	235	5.0
Crosson	5.7	27.7	5.0	2.4	0.34	12.0	275	3.6
Dickie	5.6	29.4	4.5	2.6	0.26	13.4	321	2.8
Farlain	8.0	148.0	65.0	18.3	0.03	12.0	470	3.9
Fawn	5.7	29.0	3.7	2.5	0.60	30.0	466	1.1
Georgian Bay	8.4	175.0	67.0	22.0	0.03	3.8	196	7.1
Greenbass	6.9	26.0	5.0	2.1	0.34	16.0	412	3.1
Healey	5.9	31.0	3.7	3.7	0.65	14.0	398	1.5
Heney	5.6	26.0	2.2	2.0	0.14	8.5	286	4.6
Leech	6.0	31.0	3.8	2.9	0.18	14.0	342	3.6
Leonard	5.8	35.0	2.3	2.6	0.16	6.7	298	4.5
Plastic	5.8	26.0	2.9	2.2	0.17	7.7	305	6.2
Tadenac Bay	7.7	117.0	44.0	14.2	0.09	9.7	302	3.3
Tadenac	7.0	36.0	8.0	3.4	0.15	8.0	326	3.5
Walker	6.5	35.4	7.1	3.2	0.06	6.9	293	5.6

waters (Harvey et al. 1981). Although located on the shield, Healey Lake is not a headwater lake. The three other waters, namely Georgian Bay, Tadenac Bay, and Farlain Lake, are peripheral to the shield and more highly buffered. Georgian Bay is flanked by granite bedrock along its eastern shore but partially separated from Lake Huron by the predominantly limestone Bruce Peninsula. Tadenac Bay is an indentation of Georgian Bay affected by discharges from shield lakes. Farlain Lake is situated in a predominantly limestone drainage basin (Ontario Ministry of the Environment 1973).

Water chemistry variables within the Tadenac watershed, including Greenbass Lake and Georgian Bay, were measured by the authors. Complete descriptive data for the remaining lakes were obtained from the Ontario Ministry of the Environment, Rexdale, and Dorset, Ont. and the Ontario Ministry of Natural Resources. Reported alkalinity values are total inflection point titrations. All chemical data represent whole lake values (average of samples from epilimnion, metalimnion, and hypolimnion) and are averaged from a minimum of six measurements taken at various times throughout the year. The relative percent littoral zone is derived from that proportion of the lake volume in water depth less than 6.0 m.

SAMPLE COLLECTION AND ANALYSIS

Twenty specimens of pumpkinseed were collected by angling and gill nets set in shallow water in the spring of 1981 from each location, except Georgian Bay from which only five fish were obtained. Fish were individually measured for length (±1 mm) and weight (±1 g) and sexed by examination of the gonads. Scales were removed from the area immediately posterior to the depressed left pectoral fin, washed and mounted between two glass slides, and aged on an Eberbach microprojector using 40× magnification. Scale annuli were

identified according to Regier (1962).

Comparison of sunfish growth rates between lakes was carried out by calculating the estimated mean total length at a standard age of 4+ yr. The estimated length at age 4 (EL_4) for sunfish from each lake was obtained from simple equations of length versus age where length was the dependant (y) variable. The mean condition factor (CF) of pumpkinseed from each lake was determined using the formula $CF = W/L \times 10^5$, where L = total length (centimetres) and W = weight (grams).

Whole skinless fillets of white muscle were excised from each fish and frozen in sterile plastic bags. For Hg determination, a 0.25-g aliquot of fish tissue homogenate was digested in 5 mL of 4:1 sulphuric–nitric acid mixture at 250°C for at least 3 h. Total Hg was analyzed by conventional cold-vapor UV detection with a Pharmacia mercury monitor. The working detection limit was 0.01 μg Hg/g tissue. A minimum of three surface water samples from each location were acidified to a pH of approximately 2 with concentrated nitric acid and preserved with 0.5 mL of potassium dichromate/100 mL water for subsequent Hg analysis.

Statistical Analysis

An all-possible multiple regression analysis program was employed to analyze the data statistically. The mean pumpkinseed Hg concentrations for each lake were regressed against sets of the independent environmental variables. The environmental variables considered were grouped into two basic categories:

Biological and chemical	Physical
pH	Maximum depth (Zm)
Conductivity	Mean depth (z)
Alkalinity	Lake surface area (Ao)
Calcium	Drainage area (Ad)
Total phosphorus (P)	Total catchment area ($A_T = Ad + Ao$)
Total Kjeldahl nitrogen (TKN)	Lake volume (V)
Secchi disk depth	A_T/V ratio
Growth rate (EL_4)	Littoral zone
	Morphoedaphic index (MEI)

A two-step regression analysis was conducted, as the total number of sites ($N = 16$) was too small to incorporate all independent variables in a single run. Therefore, the chemical and physical variables were regressed separately on fish Hg concentration, and the most important variables from these subsets were then combined. A number of environmental variables were highly correlated to one another, i.e. conductivity with calcium ($r = 0.99$), and therefore were not incorporated into the same regression run. Such highly confounded variables were entered into the regression analysis separately, and the best descriptor of fish Hg concentration of the pair was chosen for further computation. Furthermore, the all-possible BMDPR program used will not enter highly correlated variables into the same equation. The best subset regression equations were selected using adjusted r^2 values

TABLE 3. Morphometric characteristics of study lakes.

Lake	Depth (m)		Volume ($m^3 \times 10^5$)	Drainage basin area (ha)			Total drainage area/volume	Morphoedaphic index	Littoral zone (%)
	Maximum	Mean		Lake surface	Terrestrial catchment	Total catchment			
Basshaunt	24.0	7.7	36.6	47.3	790.6	837.9	22.8	3.8	48.3
Bigwind	32.0	10.7	118.0	111.0	389.3	500.3	4.2	1.9	47.1
Crosson	25.0	8.4	47.7	56.8	501.2	558.0	11.7	2.0	47.0
Dickie	12.0	12.0	46.4	93.2	446.6	539.8	11.6	3.8	4.8
Farlain	4.8	1.7	18.9	109.4	2401.6	2511.0	133.0	56.6	100.0
Fawn	7.9	3.4	29.1	86.7	1197.3	1284.0	44.0	5.5	80.1
Georgian Bay	—	—	—	—	—	—	—	—	—
Greenbass	9.5	4.0	5.0	12.4	40.0	52.5	10.5	4.2	80.0
Healey	7.0	2.8	33.3	119.1	1658.0	1777.1	53.4	7.2	97.0
Heney	5.8	2.8	7.2	20.1	70.9	91.0	12.6	6.0	100.0
Leech	13.7	6.3	51.6	82.1	233.9	316.0	6.1	3.1	49.9
Leonard	18.3	6.8	143.0	193.0	529.5	722.5	5.0	3.4	55.3
Plastic	16.0	8.0	31.6	31.5	88.2	119.7	2.8	2.1	33.1
Tadenac Bay	34.0	—	—	440.0	—	—	—	—	—
Tadenac	36.0	8.2	252.0	308.0	930.0	1238.0	4.9	2.8	40.0
Walker	17.0	6.2	42.1	68.2	257.6	325.8	7.7	3.7	26.0

TABLE 4. Summary of Hg concentration in pumpkinseeds from 1981 survey lakes.

Lake	Length (cm)		Weight (g)		Mean age (yr)	Estimated length at age 4 (cm)	Hg concentration (μg/g)		
	$\bar{x}$	SE	$\bar{x}$	SE			$\bar{x}$	SE	Range
Basshaunt	11.5	0.3	32.1	2.4	2.4	13.4	0.27	0.02	0.13–0.48
Bigwind	10.1	0.3	18.7	1.3	2.8	11.2	0.28	0.02	0.10–0.51
Crosson	11.8	0.3	34.9	2.8	4.2	11.4	0.33	0.02	0.20–0.52
Dickie	14.5	0.3	56.8	3.1	5.4	12.6	0.20	0.02	0.11–0.33
Farlain	14.0	0.5	66.4	9.6	3.7	14.6	0.04	0.00	0.02–0.09
Fawn	14.1	0.1	55.1	1.6	4.7	13.4	0.20	0.01	0.10–0.45
Georgian Bay	14.9	0.1	70.6	1.7	4.6	14.4	0.13	0.02	0.08–0.26
Greenbass	17.0	0.3	87.0	4.6	5.0	16.0	0.22	0.02	0.09–0.33
Healey	11.3	0.2	25.1	1.7	4.2	11.0	0.27	0.02	0.08–0.46
Heney	9.6	0.2	16.4	0.8	4.1	9.5	0.26	0.02	0.17–0.54
Leech	15.1	0.4	67.8	6.3	4.3	11.4	0.20	0.02	0.09–0.38
Leonard	10.4	0.2	25.0	1.8	2.8	11.6	0.12	0.01	0.06–0.22
Plastic	10.2	0.2	16.7	0.7	5.4	10.8	0.25	0.02	0.16–0.51
Tadenac Bay	12.5	0.4	42.0	9.8	3.6	13.4	0.12	0.04	0.04–0.30
Tadenac	13.1	0.2	48.5	2.6	3.5	13.6	0.12	0.01	0.09–0.24
Walker	14.0	0.3	60.0	3.9	3.8	14.2	0.16	0.01	0.09–0.24

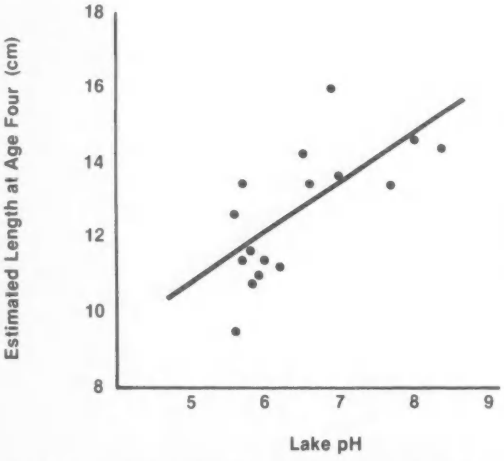

FIG. 1. Estimated total length of pumpkinseeds at age 4 (EL_4) relative to lake pH, where $EL_4 = 3.97\text{pH} + 1.34$, $r^2 = 0.69$, $P \leq 0.01$.

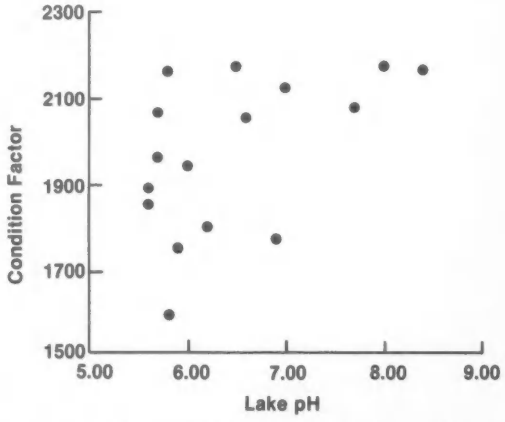

FIG. 2. Pumpkinseed condition factor (CF) in relation to lake pH, where $CF = 100.5\text{pH} + 1291.6$, $r^2 = 0.48$, $P \leq 0.10$.

and Cp plots as standard criteria (Draper and Smith 1981). Although satisfactory equations describing sunfish Hg levels were obtained, a two-step regression analysis inherently eliminates certain possible combinations of the independent variables, and it is recognized that examination of a greater number of lakes might reveal other lake conditions important to fish Hg levels.

Results

The pH of the waters sampled ranged from 5.6 to 8.4 (Table 2). Alkalinity was typically low (<10 mg/L) in all the shield lakes but was greater than 60 mg/L in Farlain Lake and Georgian Bay. Surface area of the lakes ranged from 12.4 to 308 ha (Table 3). The A_T/V ratio ranged from 2.8 to 133.0 for Farlain Lake but was generally less than 15.0 for the shield lakes.

Mean total length of the pumpkinseeds ranged from 9.6 to 17.0 cm, with a corresponding mean age ranging from 2.4 to 5.4 yr (Table 4). Between waters, the estimated fish length at age 4 (EL_4) ranged from 9.5 to 16.0 cm (Table 4). Using the EL_4 variable as a quantitative measure of fish growth rate, the data showed that growth rates of the pumpkinseeds were significantly correlated ($P < 0.01$) to lake pH, where $EL_4 = 1.34\ \text{pH} + 4.02$, $r = 0.69$ (Fig. 1). Although not as highly significant, fish condition factors (CF) were also correlated ($P < 0.10$) to lake pH, where $CF = 100.5\text{pH} + 1292$, $r = 0.48$ (Fig. 2).

Mean fish Hg concentration between lakes ranged from 0.04 to 0.33 μg/g (Table 4). Using lake pH as the sole independent environmental variable, mean fish Hg concen-

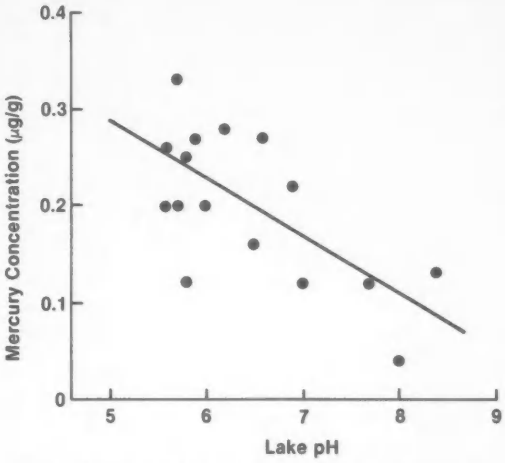

FIG. 3. Relationship of pumpkinseed mean muscle tissue Hg concentration (micrograms per gram) with pH of lakes sampled, where $Hg = -0.0569pH + 0.563$, $r^2 = -0.66$, $P \leq 0.01$.

tration (micrograms per gram) was significantly correlated ($P < 0.01$) to lake pH, as described by the simple linear equation $Hg = -0.05686pH + 0.563$, $r = -0.66$ (Fig. 3). Fish Hg concentration was also significantly correlated ($P < 0.01$) with conductivity ($r = -0.64$), alkalinity ($r = -0.63$), and Ca ($r = -0.62$). Fish Hg concentration was only significantly correlated ($P < 0.05$) with V ($r = -0.55$) of the lake morphometric variables. Tissue Hg levels were also significantly correlated ($P < 0.01$) with pumpkinseed length in Bigwind Lake ($r = 0.65$), Greenbass Lake ($r = 0.73$), and Leonard Lake ($r = 0.66$) but not in any of the other locations sampled. Total Hg concentrations in all waters were below detectable limits (0.03 μg/L).

Regression analysis of the variable subsets showed that morphometric variables alone described fish Hg concentrations much better than limnological variables alone. The best fit equation, however, was obtained by a combination of the two data sets. Combining the chemical and physical variables (Georgian Bay and Tadenac Bay not included due to lack of complete morphometric data) yielded the following equation, which incorporates Ca, maximum depth, lake volume, and littoral zone to predict pumpkinseed Hg concentration:

$$(1)\quad Hg = 0.0015LZ - 0.122Ca + 0.00914Zm - 0.00136V + 0.0975, \text{ multiple } r^2 = 0.86.$$

Although Ca was selected over pH in the regression of chemical variables only, pH in combination with the physical variables produced the following equation with a higher multiple r^2 than eq. 1:

$$(2)\quad Hg = 0.0016LZ - 0.078pH + 0.014Zm - 0.00142V + 0.492, \text{ multiple } r^2 = 0.93$$

in which Hg is mercury concentration of sunfish muscle (micrograms per gram), LZ is percent littoral zone, Ca is water calcium concentration (milligrams per litre), Zm is maximum lake depth (metres), and V is lake volume (cubic metres $\times 10^5$).

Substitution of pH for Ca did not affect selection of the other independent variables or their coefficients substantially. Examination of the standardized coefficients and T statistics for each independent variable in eq. 1 and 2 reveals that lake volume contributed the most to the models, followed by maximum depth and Ca or pH, and lastly, percent littoral zone.

Discussion

Although our findings show reduced growth rate of pumpkinseeds in lakes of lower pH, reported relationships between fish growth rate and water pH are not consistent (Spry et al. 1981; Fromm 1980). For example, increased growth rates of fish in acid-stressed lakes have been reported by Hendrey and Wright (1976) and Ryan and Harvey (1977) who attribute the phenomenon to reduced intraspecific competition resulting from recruitment failure at low pH. In contrast, a number of laboratory and field studies report reduced growth rate of fish under more acidic conditions (Beamish et al. 1975; Menendez 1976; Craig and Baksi 1977), which Spry et al. (1981) suggested may be the result of either decreased feeding or decreased food conversion ratio or a combination of both.

Decreased feeding or food availability should not be a factor limiting the growth of sunfish from lakes sampled in this study. There is no evidence that the biomass of benthic invertebrates, which constitute a significant portion of pumpkinseed diet (Scott and Crossman 1973), is reduced in acid-stressed lakes (Collins et al. 1980). Beamish (1974) also determined that food was not a limiting factor contributing to reduced growth of white suckers in acid-stressed lakes.

The trend that we observed toward decreased condition factor of pumpkinseeds in lower pH lakes suggests that fish inhabiting these waters are subject to stress. Further to the evidence of Beamish (1976) that, in addition to acid stress, fish in acidified lakes may be exposed to elevated metal levels, there is increasing evidence that the concentration of certain waterborne metals is increasing in many Precambrian Shield lakes as the result of both direct atmospheric deposition from anthropogenic sources and increased mobilization of metals from soils and sediments because of lowered lake and precipitation pH (Schneider et al. 1979; Schindler et al. 1980; Hall et al. 1980). Fraser and Harvey (1982) noted elevated levels of some metals in bones of white suckers inhabiting low-pH Ontario lakes, including one lake sampled in this study, thus providing further evidence that elevated metal levels may represent an additional physiological stress to resident fish populations.

The water Hg concentrations measured in this study (<0.03 μg/L) are generally considered normal background levels in freshwater systems (Fitzgerald 1979) and are well below concentrations observed to have any adverse effects on fish (Drummond et al. 1974; McKim et al. 1976; Snarski and Olson 1982).

Our results show that Hg concentration in pumpkinseed tissues are correlated with length in only three of the study

lakes. Although it is generally assumed that Hg concentration increases with fish size, there is evidence that indicates that differences in the correlation between Hg level and fish size exist both between and within species. For example, Koirtyohann et al. (1974) found no relationship between Hg concentration and length of bluegill sunfish (*Lepomis macrochirus*), while weak or no relationships have been reported in roach (*Rutilus rutilus*) (Bull et al. 1981), white suckers (McFarlane and Franzin 1978), and northern pike (Moore and Sutherland 1980).

Lake volume and maximum depth emerge as important variables describing Hg levels in pumpkinseed. The relative importance of these two variables should be viewed in context of their influence on water quality, which in turn can modify the biological availability of Hg within an ecosystem. Physical parameters, such as lake depth, have been directly related to lake productivity and water quality (Rawson 1952; Ryder 1965; Schindler 1971; Conroy and Keller 1976). The positive relation between percent littoral zone and Hg levels in sunfish may be partially explained by the fact that this shallow-water species would be exposed to a greater proportion of Hg-containing sediments in the epilimnion, with increased percent littoral zone.

Lake pH was not selected in the first step of the multiple regression analysis of chemical variables as having a significant contribution to sunfish Hg levels. The general postulation that reduced water pH will enhance Hg uptake by fish has been largely promoted from Hg studies that show that the more toxic methylmercury form, found in fish, is prevalent at lower water pH (Fagerstrom and Jernelov 1972; Wood 1979) and from observations of simple correlations between fish Hg levels and water pH (i.e. Fig. 3 this study; Suns et al. 1980). Some Swedish workers support this hypothesis and maintain that water concentrations of methylmercuric chloride are higher in low-pH lakes and that the concentration of this Hg compound in fish is directly related to the water concentrations (Brosset 1981). However, there is no published evidence that relates higher water Hg levels to lakes of lower pH in Canada. In unpolluted ecosystems, uptake of Hg by fish must be determined by the local bioavailability of the metal as determined by ambient environmental conditions. This is supported by Jernelov (1979) who stated that in practically any lake there is enough Hg to elevate fish Hg levels if all the biological and biochemical conditions are favorable.

Calcium emerges as one of the most important chemical variables associated with observed Hg levels in pumpkinseeds. The substantial literature detailing the interaction of Ca and metal regulation by aquatic organisms suggests that this cation may also play an important role in determining fish Hg levels. The rates of accumulation and the toxicity of several metals to fish, including Cd, Cu, Ni, Pb, and Zn, are known to be reduced by increased water hardness or Ca levels (Pickering 1974; Davies et al. 1976; Howarth and Sprague 1978; Carrol et al. 1979; Judy and Davies 1979). The mechanism to account for this effect is thought to be increased gill permeability at low Ca levels (Spry et al. 1981) or competition between metals and Ca for cellular binding sites (Zitko and Carson 1976).

In this study, water Ca concentration is negatively correlated with Hg levels in pumpkinseed. A relationship between fish Hg concentration and water Ca level was observed by McFarlane and Franzin (1980) for white suckers in five Manitoba lakes. Rodgers (1982) found that the uptake of methylmercury by rainbow trout (*Salmo gairdneri*) was less in hard water (385 mg $CaCO_3$/L) than in soft water (30 mg $CaCO_3$/L) and suggested that increased Hg uptake efficiency in soft water may partially explain elevated Hg levels observed in fish from lakes of low alkalinity and pH. The same morphometric variables were incorporated into the regression equations regardless of whether Ca or pH were used, which suggests that these two chemical variables are similarly related to fish Hg levels. Further experimental work under controlled conditions is required to delineate the relative effects of Ca and pH on Hg uptake by fish.

The equations developed in this study demonstrate that it is possible to accurately describe Hg levels in fish based on environmental variables of Precambrian Shield lakes. Although this research represents a coordinated investigation into the relationship between environmental conditions and Hg accumulation in fish, a broader data base is necessary to more rigorously test and expand the predictive capacity of the empirical models produced. The value of such models is that they are generated from standard physical and chemical data available from lake surveys. Thus, renewed field collections and tissue analysis, which are both costly and time consuming, would not be required to estimate Hg levels in a given indicator fish species from a particular lake or set of lakes.

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NOTES

Selection by Young Rainbow Trout (*Salmo gairdneri*) in Simulated Stream Environments For Live and Dead Prey of Different Sizes

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IRVINE, J. R., AND T. G. NORTHCOTE. 1983. Selection by young rainbow trout (*Salmo gairdneri*) in simulated stream environments for live and dead prey of different sizes. Can. J. Fish. Aquat. Sci. 40: 1745–1749.

Underyearling rainbow trout (*Salmo gairdneri*) in experimental stream tanks presented with live and dead prey preferred live prey. Trout fry generally were size selective predators and previous feeding experience did not affect the size of prey consumed. When a wide range of prey sizes was offered, larger trout fry fed upon bigger prey than did smaller fry. *Cyclops* were underrepresented in trout fry stomachs relative to *Daphnia* of similar size.

IRVINE, J. R., AND T. G. NORTHCOTE. 1983. Selection by young rainbow trout (*Salmo gairdneri*) in simulated stream environments for live and dead prey of different sizes. Can. J. Fish. Aquat. Sci. 40: 1745–1749.

En présence de proies vivantes et mortes, des truites arc-en-ciel (*Salmo gairdneri*) de moins d'un an maintenus en bassins expérimentaux simulant un cours d'eau préfèrent les proies vivantes. En général, les truitelles sont des prédateurs sélectifs et l'expérience n'influe pas sur la taille de la proie ingérée. Quand on leur offre une gamme étendue de tailles des proies, les grands alevins saisissent des proies plus grosses comparativement aux petits alevins. Les *Cyclops* sont sous-représentés dans les estomacs d'alevins de truite par rapport aux *Daphnia* de même taille.

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SINCE the classic paper by Brooks and Dodson (1965), size-selective predation has been demonstrated many times in lake fishes but less frequently in drift-feeding stream salmonids (Ringler 1979). The feeding of planktivorous lake fishes has received the most attention, with prey size frequency distributions and different rates of capture success often used in models explaining predator selectivities (Werner and Hall 1974; Confer and Blades 1975; O'Brien et al. 1976; Eggers 1977). No such feeding models have been developed for stream fishes, and only recently (Ringler 1979; Waňkowski 1979; Waňkowski and Thorpe 1979) have experimental studies been undertaken to test prey size and predator selection relationships.

We examined in stream tanks some aspects of prey acquisition by juvenile rainbow trout from the Lardeau River in southeastern British Columbia. Experiments tested hypotheses formulated during the study of the fish in their natural stream environment, using prey similar to those eaten in nature. In the Lardeau River, we found that trout fry usually rose in the water column to feed on drifting prey, and generally were size selective predators (Irvine and Northcote 1982). However, because *Cyclops bicuspidatus* were underrepresented in the trout fry stomachs compared to similar sized *Daphnia galeata mendotae*, we suggested that prey body movement might affect predator selectivity. We therefore examined the importance of prey movement experimentally by testing the hypothesis that there would be no difference in numbers consumed of live and dead prey of the same species. Because trout fry in the Lardeau River shifted from feeding predominantly on zooplankters to larger, immature aquatic insects as they grew (Irvine and Northcote 1982), we conducted experiments to determine the effects of fry feeding experience and size on prey selection. The effects of feeding experience were examined by testing the hypothesis that there would be no difference between the size of prey eaten by small trout fry with and without previous feeding experience. The effects of fish size were examined by testing the hypothesis that there would be no difference between the size of prey eaten by two sizes of underyearling trout with the same feeding experience. Prey selection in stream tanks was compared with that in the Lardeau River by testing three sizes of underyearling trout (each with different feeding experience) with prey similar to that utilized in the river.

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Materials and methods — All fry were Lardeau/Duncan stock rainbow trout that overwinter in this British Columbian river system (Irvine 1978). The fishes' previous feeding experience was one of three types: (1) naive — fry raised in incubation boxes and used immediately after emergence with no feeding experience (29 mm mean fork length); (2) hatchery — fry raised in a hatchery and exposed only to hatchery food (34 mm mean length); (3) river-fed — fry captured from the Lardeau River and with previous feeding experience on natural food types and either recently emerged (31 mm mean length) or older (41 mm mean length).

Prey taxa (size ranges in parentheses) used in the experiments were blackfly larvae (*Simulium* spp.; 0.2−7.2 mm), ephemeropteran (Heptageniidae) nymphs (3.5−6.5 mm), *Daphnia rosea* (1.6−2.3 mm), *Ceriodaphnia pulchella* (1.0−1.5 mm), and a mixture of zooplankters comprised primarily of *Bosmina longirostris, Daphnia galeata mendotae, Cyclops bicuspidatus,* and *Diaptomus* spp. One experiment used intermediate sized blackfly larvae (3.5−6.5 mm) which were isolated using a series of graded sized sieves (0.25−1.25 mm mesh). Live prey were collected just prior to experiments to ensure that animals were alive during the experiments. All dead prey were killed by freezing. We could see no difference in color or shading between live and dead organisms. Prey body lengths were measured as the longest dimension exclusive of antennae, cerci or any extended appendage.

All experiments were performed in recirculating octagonal plexiglass stream tanks within a channel 3.4 m long, 17 cm wide with a water depth of 20 cm (116 L). Water temperature ranged between 11 and 13°C. To ensure the only food available to fish was that intended, strained (130 μm mesh) spring water was used in the tanks for all experiments and the rocks used to simulate a natural stream bottom were scrubbed and rinsed before being placed on the bottoms of the tanks. Screens (1.25 mm mesh) over the tanks reduced the possibility of airborne insects entering.

Between 26 and 34 fish were introduced to each tank at about 1800 h. Several hours later, water current was initiated by submersible electric pumps to maintain a surface water velocity of approximately 10 cm/s. Fish were not fed for 41 h to allow previously consumed food to become digested, and to reduce individual variations in hunger level. At this time, 1.5 g of dry Chinook Mash hatchery food were introduced to each tank to reduce fry hunger levels to a more natural state.

Near midday, 42 h after fish had been introduced, prey were mixed with water and poured through funnels into four of the corners of the stream tanks. Prey were added every 5 min for 1 h. Turbulence in the stream tanks rapidly distributed most prey types throughout the water column. Fry continued to feed throughout all experiments. At the end of each experiment, fry were removed from the stream tanks, immediately killed and preserved in 10% formalin. Stomach contents of the fry were later analyzed to determine electivity values [$E = (Ri - Pi)/(Ri + Pi)$, where Ri = proportion of taxon i in the diet and Pi = its proportion in the environment] (Ivlev 1961).

Live versus dead prey — Two separate experiments tested for differences in numbers consumed of live and dead prey of the same species. In the first experiment, one group of hatchery trout fry was provided 225 dead *Ceriodaphnia* and 225 dead *Daphnia* every 5 min. The feeding of these fry was compared with a separate group of hatchery fry which were provided the same numbers and types of prey taxa, but *Ceriodaphnia* were alive and *Daphnia* dead. In a second experiment, one group of recently emerged river-fed dry was fed 250 dead intermediate sized *Simulium* and 250 dead Heptageniidae nymphs every 5 min. The feeding of these fry was compared with a second group which were provided the same prey, only *Simulium* were alive and Heptageniidae nymphs dead.

TABLE 1. Prey consumed by hatchery and recently emerged river-fed rainbow trout fry in experiments testing for differences in numbers consumed of live and dead prey. Mean number of prey per fish in parentheses.

Feeding experience	Total prey consumed		
	Ceriodaphnia		*Daphnia*
	Live	Dead	Dead
Hatchery	—	152 (5.6)	102 (3.9)
Hatchery	574 (16.9)	—	184 (5.4)
	Simulium		Heptageniidae
	Live	Dead	Dead
River-fed	—	113 (3.7)	250 (8.1)
River-fed	262 (8.5)	—	132 (4.3)

Fry feeding experience and fry size — To determine the effects of previous feeding experience and fry size on prey selection, 200 dead *Simulium* were presented every 5 min to trout fry. The size distribution of *Simulium* consumed by recently emerged river-fed fry was compared with that of naive fry to evaluate the effects of fry feeding experience. The size distribution of *Simulium* eaten by recently emerged river-fed fry was then compared with that of older river-fed fry to determine the effects of fry size.

Feeding of fry in stream tanks and the Lardeau River — Naive, hatchery and older river-fed fry were provided a mixture of live zooplankters and prey selection by these fish compared with selection by rainbow trout fry feeding in the upper Lardeau River (Irvine and Northcote 1982). Prey added to stream tanks every 5 min were those filtered in 250 m^3 of water from the outlet of Trout Lake, which flows into the upper Lardeau River. Two extra samples were taken at the beginning and end of each experiment to determine species compositions and numbers of prey introduced for that experiment.

Results — Live versus dead prey — Trout fry with and without previous exposure to live prey consumed more prey

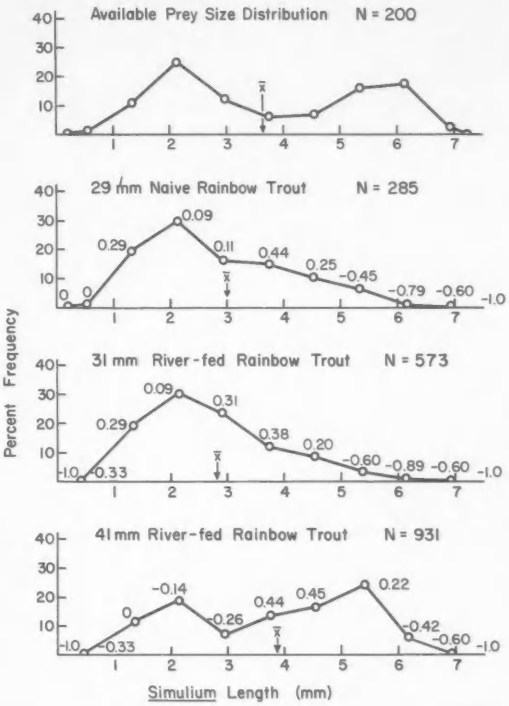

FIG. 1. Length frequency of *Simulium* larvae available to, and consumed by, rainbow trout (*Salmo gairdneri*) fry. Electivity values for each prey size are given.

when that prey was alive than when it was dead (Table 1; χ^2-tests; $P < 0.05$ in both cases). When given a choice of feeding upon dead *Ceriodaphnia* or dead *Daphnia*, hatchery fry consumed more *Ceriodaphnia*. When live *Ceriodaphnia* were used in place of dead *Ceriodaphnia*, significantly more *Ceriodaphnia* were eaten than previously. When recently emerged river-fed fry were provided equal numbers of dead Heptageniidae and dead *Simulium*, approximately twice as many Heptageniidae were consumed as *Simulium*. When live instead of dead *Simulium* were used along with equal numbers of dead Heptageniidae, the reverse was found with significantly more *Simulium* being consumed.

The location of prey capture in the water column of the stream tanks was similar to that observed in the Lardeau River (Irvine and Northcote 1982). In both cases, the majority of feeding strikes were directed at prey drifting in the water column above the holding position of the fish. In stream tanks live *Simulium* settled out more rapidly than dead *Simulium*. Because fry rarely fed off the bottom, the availability of live *Simulium* to feeding fry was reduced, and enhanced the significance of the above results.

Fry feeding experience and fry size — When a wide range of sizes of *Simulium* larvae were offered as potential prey to young rainbow trout, the previous feeding history of the trout did not affect the size of prey consumed, but the size of the fish did. There was no difference between the size distribution of *Simulium* eaten by naive (29 mm) fry and recently emerged (31 mm) river-fed fry (Fig. 1). Positive electivities were obtained for both these groups of fry for prey ranging in size from 1.0 to 4.5 mm and negative values for prey greater than 5.0 mm. Older (41 mm) river-fed trout were larger than either group of smaller trout and consumed bigger prey (paired *t*-tests; $P < 0.05$ in each case). Older river-fed fry had positive electivities for prey between 3.5–5.5 mm and negative or zero electivities for prey outside this range (Fig. 1).

TABLE 2. Mean electivities and lengths (ranges in parentheses) for zooplankton consumed by naive, hatchery and older river-fed rainbow trout fry.

Feeding experience	Zooplankter	Electivity	Length, mm (n = 15)
Naive	*Daphnia*	0.70	0.26 (0.22–0.30)
	Cyclops	−0.71	0.27 (0.24–0.30)
	Bosmina	−0.89	0.15 (0.12–0.20)
Hatchery	*Diaptomus*	0.89	0.51 (0.42–0.66)
	Daphnia	0.75	0.34 (0.28–0.42)
	Cyclops	−0.49	0.28 (0.22–0.36)
River-fed	*Diaptomus*	0.97	0.53 (0.48–0.60)
	Daphnia	0.80	0.29 (0.24–0.38)
	Cyclops	−0.20	0.32 (0.28–0.38)
	Bosmina	−0.54	0.15 (0.12–0.20)

Feeding of fry in stream tanks and the Lardeau River — Prey compositions varied between experiments with *Diaptomus* unavailable to naive fry and *Bosmina* unavailable to hatchery fry (Table 2). When present, *Bosmina*, a small prey item, was consumed less and *Daphnia* and *Diaptomus*, both larger prey items, were consumed more than proportionately to their abundance. *Cyclops*, a prey item similar in size to *Daphnia*, was underrepresented in the stomachs. In the upper Lardeau River positive electivities were also obtained for large calanoid copepods and *Daphnia* and negative electivities for *Bosmina* and *Cyclops* (Irvine and Northcote 1982).

Discussion — Our experiments examining the effects of prey body movement assumed the chief difference between live prey, and prey killed by freezing, was body movement. This conclusion was reached after considering the eight prey characteristics Nilsson (1978) listed as important in trout feeding. Of these eight properties, prey color, size and structure were not altered by freezing, at least to the human eye. A fourth prey characteristic, their availability, was in fact greater for one prey (*Simulium*) in our stream tanks when dead than alive. Prey density would not have been affected by freezing and palatability did not appear to be since prey rejection was not common. Prey odor could have been altered by freezing, but since fry generally moved up in the water column to feed, they were not likely in an area where chemical cues were important. Only the final prey characteristic, its escape or movement behavior, would have been destroyed by freezing.

Because significantly more live than dead prey were

consumed by trout fry (Table 1), we concluded that body movement is an important prey characteristic to stream rearing trout. Since both trout with and without previous exposure to live moving prey fed upon more live than dead prey, it appears the preference for moving prey is innate. Both Ware (1973) and Bryan (1973) had previously demonstrated the importance of prey movement to rainbow trout, but their experiments were in standing water aquaria. In any stream, fish are presented with many drifting objects within the size range upon which they can feed. Many of these provide little or no nutritional benefit (e.g. inorganic material). Live items which should be energetically more profitable to consume will usually exhibit some degree of body movement while nonliving objects will not. It seems likely that the survival rate of young salmonids feeding upon active and hence generally more nutritional food types would be greater than those feeding on nonmoving items.

There was no difference in the size of *Simulium* larvae consumed by fry with no previous feeding experience and similar sized fry with experience feeding on natural prey (Fig. 1). Fish size did affect prey size since larger river-fed fry generally consumed bigger prey than naive or recently emerged river-fed fry. For all predators, prey organisms will lie within a discrete size range. Below a threshold size, predation is negligible because prey are too small either to be seen or to be energetically profitable to consume. Above this size threshold, predation increases with increasing prey size (Hall et al. 1976) until some critical prey size is reached above which physical limitations of the predator prevent prey ingestion.

Fish size did not affect prey size when fish were offered unsorted live zooplankton, presumably because all prey were small. The same feeding patterns were found for trout exposed to live zooplankton in stream tanks as trout in the upper Lardeau River (Irvine and Northcote 1982). Size selective predation occurred with positive electivities obtained for large calanoid copepods and *Daphnia* and negative electivities for smaller *Bosmina*. However *Cyclops*, similar in size to *Daphnia*, were always underrepresented in fry stomachs. The fact that both naive and experienced trout consumed more *Daphnia* than similar sized *Cyclops* implies that the general preference found by a number of workers for cladocerans over copepods in fish feeding (Galbraith 1967; Brooks 1968; Craddock et al. 1976) is not a learned response as suggested by Vinyard (1980), but rather a response due to differential properties of the prey. Although other possible explanations exist, it seems likely that *Cyclops* have a better escape response than *Daphnia*. Brook and Woodward (1956) and Schröder (1967) have shown *Cyclops* to have positive rheotactic behavior and Drenner et al. (1978) found *Cyclops* were significantly better at avoiding predators than *Daphnia*.

Although our fish were size selective predators, they did not feed upon only large prey. Neither did they always consume prey proportionately to their abundance. Thus it appears that feeding models having as their primary inputs encounter frequency (Confer and Blades 1975) and/or real or apparent prey size (Werner and Hall 1974; O'Brien et al. 1976; Eggers 1977) are not adequate for stream dwelling salmonids. There is a need for further experimental feeding studies of stream fish before a model can be developed incorporating relevant inputs from lake models, but also stressing processes applicable to the stream environment. Our study suggests that prey body movement should be used as one of the primary model inputs to explain predator selectivity in stream feeding fishes.

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Introduction to Large-Scale Comparative Studies of Lakes[1]

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EVERY science seeks explanatory theories that are sufficiently general to predict and explain the behavior of a wide range of similar systems. The explanations may be generated by studies of single systems or subsystems, or by broader-scale comparisons among systems. Whereas extrapolation from detailed small-scale studies may or may not be valid, the patterns reported for large-scale studies are, by definition, significant generalizations about system characteristics. The conviction that limnologists have not adequately exploited the potential of such large-scale comparative studies for integrating ideas and testing hypotheses led, in 1977, to the Lake Ecosystem Working Group (LEWG) study at the University of Toronto. Our goal was to gather a comprehensive physical, chemical, and biological database on about 40 Ontario lakes so that we could test existing hypotheses (most of which had been generated by smaller-scale studies), and establish empirical relationships between lake ecosystem structure and stresses such as fisheries exploitation, acidification, and nutrient loading. After 3 years of data collection, we invited participants in other large-scale studies to join us in a symposium to discuss some of the general patterns revealed by the broad-scale comparative approach. The following group of 10 papers grew from that meeting.

These papers illustrate the strength of the approach in both the generation and refinement of scientific hypotheses. Three aspects of this process are exemplified. First, comparative studies often require the formulation of new variables for comparing and classifying systems. Clearly, only those variables that ultimately provide insight into system organization and function are useful. The paper by Gates et al. represents an attempt to define variables useful in characterizing temporal changes in the plankton community by documenting striking similarities among lakes through between-year changes in plankton biomass distributions. Sprules et al. have introduced to lake studies a quantitative treatment of particle-size patterns that were originally recognized in marine systems. Both Peters and Sprules et al. emphasize the predictive power of particle-size theory in lakes. Lewis, in an effort to resolve increasingly obvious inadequacies in the original classification of lakes by annual mixing regime, introduces a more generally applicable and precise terminology which preserves as much of the established usage as possible.

A second feature of the comparative approach is empirical modeling, i.e. the establishment of statistical relationships among variables in a large dataset. This empirical approach particularly highlights the value of studies across many lakes, because it focuses on influences powerful enough to stand out against a background of extensive among-lake variation in other parameters. Only from large-scale studies can we begin to appreciate the relative importance of the variables that may influence structure and processes in any one lake. For example, small-scale studies of one or two lakes have repeatedly provided evidence that planktivory affects the size distribution of zooplankton. However, only a larger-scale study like that of L. B. Holtby, W. G. Sprules, H. H. Harvey, and A. P. Zimmerman (unpublished data) can determine whether planktivory is the major determinant of zooplankton community size structure, or whether it merely moderates the effects of more powerful variables.

The variable reduction and empirical modeling processes are represented by several papers in this set. Zimmerman et al. report an improvement in phosphorus–phytoplankton regressions within lake groups derived from a typology based on multivariate measures of lake morphometry and chemistry. Paloheimo and Zimmerman show that the yield of phytoplankton per unit phosphorus is more directly related to phytoplankton–zooplankton interactions than to chemical or geological features of lakes. Gates et al. report that annual changes in the size structure of zooplankton communities are dominated by alterations in the abundance of netphytoplankton, which are strongly correlated with between-year variation in precipitation and flushing time.

The refinement of empirical relationships that leads toward explanatory theory constitutes a third aspect of the comparative approach. Bays and Crisman, for instance, find the expected positive relationships between zooplankton biomass and lake trophy, and are able to considerably refine hypotheses about the basis for the pattern. Collins et al. contend that low catches of crayfish in passive traps in lakes with abundant predatory fish result largely from behavioral changes that reduce crayfish trapability, not from reductions in crayfish density.

The papers of Schlesinger and Regier and Shuter et al. illustrate how comparisons of results on different spatial scales can be useful. The first paper compares the relationship between fish growth and temperature at two different spatial scales. Whereas temperature has a fundamental influence on growth in laboratory systems, regressions of water temperature on fish yield across many lakes are not usually statistically significant. Insights into the structure of fish communities arise from an examination of this paradox. Shuter et al. compare results from analyses on different spatial scales in an effort to confront one of the most difficult aspects of large-scale statistical analysis — distinguishing causation from mere correlation.

The statistical aspect of large-scale aquatic studies deserves further discussion. When large numbers of variables are involved, it becomes difficult to separate spurious from real correlations, because the number of chance correlations is appreciable. A realistic approach to this problem is to remain sceptical of the validity of relationships until they are shown

[1]Introduction to a sequential set of papers growing out of a special symposium on Large-Scale Comparative Studies of Aquatic Systems which was held at the June 1982 annual meeting of the American Society of Limnology and Oceanography in Raleigh, North Carolina.

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to be consistent across a number of independent datasets. Another problem is that precision in large-scale studies is necessarily lower than is possible in small-scale studies, both because a much greater range of variation in uncontrolled variables is incorporated, and because there is usually a trade-off between the spatial scale of a study and the intensity of sampling in any one lake. The comparatively low explained variances characteristic of regressions in large-scale studies are often criticized unfairly by those who mistakenly view these regression models as the end rather than the beginning of serious study. In our view this modest explanatory power more accurately reflects our current predictive abilities in limnology than do the much higher coefficients of determination commonly encountered in smaller-scale studies.

Acknowledgments

We particularly express our appreciation to the organizers of the Raleigh, North Carolina meetings for supporting our symposium, to the original participants in the symposium and the authors of the papers printed here, and to the editorial team for support throughout the critical refereeing and revision of the manuscripts to final primary publication 16 months after the symposium.

Planktonic Biomass Trajectories in Lake Ecosystems[1]

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GATES, M. A., A. P. ZIMMERMAN, W. G. SPRULES, AND R. KNOECHEL. 1983. Planktonic biomass trajectories in lake ecosystems. Can. J. Fish. Aquat. Sci. 40: 1752 – 1760.

We introduce a method, based on principal components analysis, for studying temporal changes in biomass allocation among 16 size–category compartments of lake plankton. Applied to data from a series of 12 Ontario lakes over three sampling seasons, the technique provides a simple means of visualizing shifts in patterns of biomass allocation, and it allows comparative analyses of biomass fluctuations in different lakes. Each of the primary component axes is interpretable. Furthermore, a large proportion of the variance in both the mean position of a lake and its movement along these axes is interpreted as a function of lake physicochemistry. The analysis also provides weighted scores for use in hypothesis testing which are an improvement over mean biomass values alone, because they take into account the structure of variation in the data set.

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Les auteurs présentent une méthode basée sur l'analyse des composantes principales pour l'étude des variations temporelles de la répartition de la biomasse parmi 16 catégories de taille du plancton lacustre. La technique, appliquée aux données recueillies dans 12 lacs ontariens pendant trois saisons d'échantillonnage, constitue un moyen simple pour visualiser les modifications des schèmes de répartition de la biomasse et permet des analyses comparatives des variations de la biomasse dans différents lacs. On peut interpréter chacune des axes de la composante primaire. De plus, une grande partie de la variance de la position moyenne d'un lac et de son déplacement le long de ces axes est interprétée comme une fonction de la chimie physique du lac. L'analyse fournit aussi des valeurs pondérées pour la vérification d'une hypothèse, lesquelles valeurs constituent une amélioration par rapport aux valeurs moyennes de la biomasse parce qu'elles tiennent compte de la structure de la variation de l'ensemble des données.

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A primary constituent of lake ecosystems is the planktonic compartment, which in any given set of lakes is comprised of a large variety of taxonomic types. These plankters traditionally have been divided into phytoplankton and zooplankton to separate primarily autotrophic from primarily heterotrophic organisms, and thus to approach a more meaningful classification of the planktonic biota.

Further subdivision of these two broad categories along a size continuum, irrespective of taxonomic boundaries, has proven a useful perspective on plankton dynamics for comparative studies of a number of different lake ecosystems (Sprules and Holtby 1979; Mills and Schiavone 1982; Sprules and Knoechel 1983; Harris 1980; Paloheimo et al. 1983). Furthermore, knowledge of relative biomass allocation among plankton compartments should lead to improved knowledge of the growth and production efficiencies and of relative biomass allocation in the next link in the planktonic food web, namely the fish compartment(s). However, the relative allocation of biomass to different planktonic size compartments within a given lake changes, often dramatically, from week to week and from season to season (Paloheimo et al. 1983), and in such a way that even seasonally averaged patterns can vary from year to year. Clearly, such temporal instability frustrates the comparative study of lakes.

Our approach has been to study recurring patterns in the temporal variations themselves. As biomass shifts from one set of size categories to another, we have attempted to find consistencies in the pattern of these shifts. Here we present a multivariate ordination method for analyzing these temporal variations in biomass allocation among planktonic size compartments, and we apply the method to data from a series of Ontario lakes.

Previous multivariate studies of temporal trends in phytoplankton (Allen et al. 1977; Bartell et al. 1978; Harris and

[1]This contribution is one of a sequential set of papers growing out of a special symposium on Large-Scale Comparative Studies of Aquatic Systems which was held at the June 1982 annual meeting of the American Society of Limnology and Oceanography in Raleigh, North Carolina.

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Piccinin 1980) and zooplankton (Sprules 1977) communities have been based on ordinations of species abundances or shifts in species abundances. Such studies, as well as being dependent upon the particular species lists used in each study, are well known inherently to lack analytical stability (being sensitive to slight fluctuations in the data) and to create artificial distortion (Green 1979, section 4.4; Gauch 1983). In addition, ordinations based on taxonomic variables commonly do not extract large proportions of the total variation in the first few component axes. Thus, Allen et al. (1977) extracted only 15% of the variation in the first two principal components based on "first differences" of species abundances; Bartell et al. (1978) achieved only 36%, again based on first differences; Sprules (1977), using normalized proportional species abundances (and thus effectively reducing the analysis to only a few numerically dominant species), was able to achieve 49, 65, and 58% extraction in data from three separate sets of lakes; whereas Harris and Piccinin (1980) did not report variance extracted nor any other details of the eigenstructure, and so there is no way to judge the analytical effectiveness of their procedure.

Our approach is to use proportional biomass variables for size classes of plankton. This yields a taxonomy-independent approach, based on analytically robust variables, that is applicable to the plankton of any lake, in any part of the world. Furthermore, we have succeeded in extracting a large proportion of the total variance, and we are able to obtain useful interpretations for our components. To our knowledge, this is also the first time that an ordination procedure has been applied to the total phytoplankton and zooplankton communities of lakes.

Materials and Methods

Data Collection

Table 1 lists summary limnological information for the set of Ontario lakes that were sampled fortnightly during the ice-free periods of 1978, 1979, and 1980. A more detailed description of the physicochemistry of these lakes is given in Zimmerman et al. (1983).

Physicochemical, phytoplankton, and zooplankton samples were taken at the deepest part in the major basin of each lake. Depth profiles of temperature, pH, conductivity, oxidation reduction potential, and dissolved oxygen levels were taken with a Hydrolab Surveyor. Light levels were determined with a Canadian Research Institute model DPMT-100 photometer. A Secchi disk was used to determine transparency. Epilimnetic composite samples were taken for phytoplankton with an integrated tube sampler, whereas zooplankton samples were obtained with a metered conical tow net hauled from near bottom to the surface.

Lugol's iodine-preserved phytoplankton samples were settled, made into permanent slides (Knoechel and Kalff 1976), and individual algae were measured under phase microscopy. Volumes were calculated from standard geometric formulae and converted into biomass estimates. Four functional size classes (see Table 2) for spherical cells and colonies were used and two for filamentous algae.

Subsamples of preserved zooplankton samples were placed

Table 1. Mean values of some limnological parameters for a series of Ontario lakes during the ice-free periods of 1978 and 1979.

Name	Location Lat. (°N)	Location Long. (°W)	Mean depth (m)	Maximum depth (m)	Surface area (km^2)	Secchi depth (m)	Total [P] ($\mu g \cdot L^{-1}$)	Volume (millions of m^3)	pH	Conductivity ($mS \cdot m^{-1}$)	Dissolved oxygen ($mg \cdot L^{-1}$)	Organic carbon ($mg \cdot L^{-1}$)	Inorganic carbon ($mg \cdot L^{-1}$)	Kjeldahl nitrogen ($mg \cdot L^{-1}$)	Total biomass ($\mu g \cdot L^{-1}$)
M2	45°12′	78°56′	9.37	21.9	0.50	6.7	5	4.7	6.45	2.5	8.9	5.8	1.0	0.18	1619.8
M3	45°03′	78°50′	4.56	11.6	0.89	2.8	12	4.1	6.32	2.8	8.7	5.8	1.0	0.35	2484.2
M4	45°05′	79°02′	8.15	23.5	0.59	3.9	7	4.8	5.82	2.3	8.8	4.0	0.6	0.25	991.8
M5	45°59′	78°43′	13.43	31.4	3.19	5.8	2	44.2	7.17	4.5	9.3	3.2	2.3	0.21	1057.0
M6	45°11′	78°50′	8.10	16.8	0.33	6.4	3	2.6	5.43	1.8	9.0	2.5	0.6	0.19	1730.4
M8	45°10′	79°27′	3.48	11.0	9.29	2.9	16	32.3	7.53	5.0	8.6	5.1	2.6	0.47	2773.8
N4	45°53′	79°30′	2.56	5.8	0.29	2.7	9	0.7	5.50	2.5	8.6	5.8	0.8	0.35	1979.2
N5	46°01′	79°31′	5.72	14.6	1.97	4.7	5	11.3	6.45	3.4	8.9	5.0	1.0	0.27	992.0
O1	44°36′	79°30′	3.47	13.7	5.42	2.1	27	18.8	8.28	23.2	9.1	5.2	33.6	0.43	6247.8
O2	44°41′	78°45′	8.47	19.2	7.86	6.0	7	66.5	8.11	17.7	9.0	4.9	25.5	0.29	1133.8
O5	44°43′	79°10′	4.33	10.4	0.93	3.3	12	4.0	8.23	17.8	9.1	5.6	19.8	0.41	3064.3
S7	46°07′	81°07′	11.87	39.6	11.42	4.8	3	135.7	4.85	3.7	9.0	3.3	0.2	0.20	677.0

TABLE 2. List of 16 functional biomass size classes used in the trajectory analysis, grouped by four broad descriptive categories: edible and inedible phytoplankton,[a] herbivorous and carnivorous zooplankton. Sizes of phytoplankton are given in terms of the maximum equivalent spherical diameter. Zooplankton sizes are in terms of maximum body length.

Description	Size (in μm)
Edible 1	<2
Edible 2	2–5
Edible 3	5–10
Edible 4	10–30
Inedible 1	>30
Inedible 2	Filaments
Herbivore 1	<300
Herbivore 2	300–500
Herbivore 3	500–850
Herbivore 4	850–1200
Herbivore 5	>1200
Carnivore 1	<500
Carnivore 2	500–900
Carnivore 3	900–1200
Carnivore 4	1200–1500
Carnivore 5	>1500

[a]For convenience, the four nannoplankton size classes have been summed and designated "edible," whereas net plankton are designated "inedible" (Sprules and Knoechel 1983).

in circular counting chambers, and individual plankters were measured with electronic calipers from projected images under phase microscopy. Specimens were classed as herbivores or carnivores and placed into one of five functional size categories (Table 2) for each type (Sprules et al. 1983). Biomass was estimated from regressions of wet weight on length for each category. Criteria for the size categories of both phytoplankton and zooplankton and further methodological details are given elsewhere (Sprules and Knoechel 1983).

DATA ANALYSIS

All data were entered onto magnetic disk memory and processed on the University of Toronto's IBM 3033 Processor system, using FORTRAN programs written by M. Gates or existing programs in the SAS (SAS Institute, Inc., Cary, NC) and BMDP (Health Sciences Computing Facility, University of California, Los Angeles, CA) libraries. For each of the lakes and for each sampling period, data for the biomass in each of the 16 size classes of plankton given in Table 2 were expressed as proportions of the total biomass (the sum of all 16 classes). Thus, for each variable, there were 96 observations for each year.

The total matrix (all lakes over all sampling times) of covariances among the 16 proportional biomass variables was subjected to principal components analysis (Morrison 1967; Tatsuoka 1971; Gates 1983), whereby the eigenvalues and eigenvectors of this covariance matrix are extracted numerically. (A covariance matrix analysis was used because all variables are in the same units and because it will extract more information than one based on correlations only.) In this procedure, each new component is a unique linear combination of the original 16 variables. Furthermore, the first component contains the largest share of the statistical variation in the original data set, whereas the second is uncorrelated and independent of the first and contains the second largest amount of variation. Subsequent components, each unique and uncorrelated with the preceding ones, express decreasing amounts of the total variation in the data. The exact composition of each component in terms of the original variables can be determined from the correlations of each new component with the original variables; these correlations are, in fact, precisely the coefficients in the linear combination of variables that defines each component.

The result of this procedure is a rigid rotation of the data as represented in 16-dimensional space, so that the first new axis, called principal component 1 (hereafter, PC 1), is the "longest", with the most variation in the data along its length, whereas PC 2 is perpendicular to PC 1 and has the second most variation, etc. By replotting the data in the space defined by the first few principal components, most of the variation in the data usually will be represented in a space of low dimensionality, with little loss of information.

Because our data correspond, for each of the 12 lakes, to a series of points in time, biomass trajectories can be constructed by joining corresponding points in this dimensionally reduced principal component space. Each lake will have a unique path or trajectory in this space, and these trajectories can be compared between years and among lakes. Furthermore, the data points for 1980 then can be projected into this space as well, to assess the robustness of the analysis. If the 1980 trajectories were to lie completely outside the subspace defined by the 1978 and 1979 analysis, this would indicate that biomass variations (as measured by allocation to 16 size classes) were too extreme to be captured by this method of analysis.

Correlation analyses were performed to explore the strength of our intrpretations of the components, as judged by inspection of their coefficients. Finally, to interpret the trajectory patterns themselves, we regressed the component scores against various physicochemical variables.

The above principal component analyses also were performed on the raw biomass data matrix, but these analyses explained proportionately less total variation per component and were not as easily interpretable. Our results indicate that analyses based on proportional biomass variables are inherently more stable. Furthermore, they will be more broadly applicable to other lake sets, as they are less dependent upon the absolute magnitudes of biomass fluctuations.

Results and Discussion

BIOMASS FLUCTUATIONS

The amount of biomass in each of the 16 size categories fluctuated in each lake from one sampling period to another. Figure 1 illustrates the extent of temporal variations in the four broad biomass categories of Table 2 for 1978, 1979, and 1980

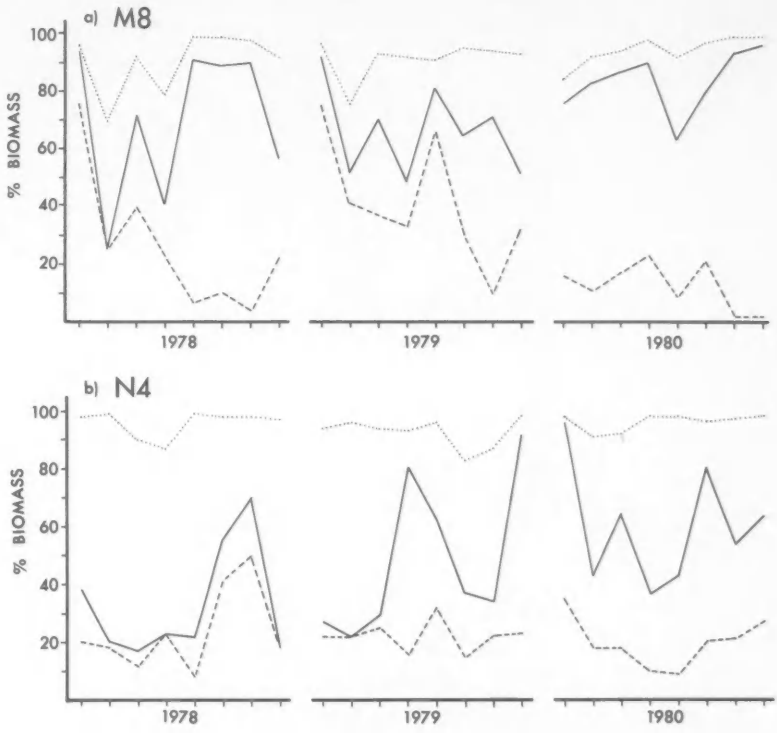

FIG. 1. Temporal variation in cumulative proportions of biomass in four broad categories for two representative lakes during 1978, 1979, and 1980: (a) M8, (b) N4. Dashed lines indicate the proportion of edible phytoplankton; solid lines, edible plus inedible; dotted lines, edible plus inedible plus herbivores.

for two lakes, N4 and M8.

These examples illustrate the great amount of variation which can occur in biomass allocation, even in relatively broad units, within a given lake over a given summer. It was to reduce this variability to more manageable proportions that principal components analysis was undertaken.

BIOMASS TRAJECTORIES

Using the covariance matrix for the relative allocation of biomass to 16 size categories, the first two principal components account for 73% of the total variation in the data, with 58% in the first principal component. Biomass trajectories in the space defined by these first two components for lake M8 in 1978 and 1979 are presented in Fig. 2. This example, which was typical of all our lakes, shows that the 2 yr differed both in the mean position and in the direction of biomass shifts.

Inclusion of the data for the 3rd year, 1980, in the analysis demonstrates the stability of the trajectory representation of biomass fluctuations. Figures 3 and 4 show the results for two quite different lakes, M5 and N4 (see Table 1). It is clear that biomass trajectory patterns in these three representative lakes (M8, M5, and N5) are quite different.

Also shown (in Fig. 3 and 4) are biomass pies illustrating the relative allocation of biomass in four broad categories: edible and inedible phytoplankton, herbivorous and carnivorous zooplankton. The size of the wedges corresponds to the relative amount of biomass in each category.

Thus, 1980 was a year in which total biomass increased in both lakes, but much more so in N4 than in M5. There also is a trend across all 3 yr for a proportionate increase in the amount of inedible phytoplankton, with a resultant shift in the biomass allocation trajectory from year to year.

Indeed, this shift was seen in all of the sampled lakes, as indicated in Fig. 5, which plots the mean biomass position for each year in the same space. It is clear that most lakes move in the same direction along the first principal component, with the exception of the two lakes which have the highest absolute amounts of biomass, M8 and O1.

A last step in the reduction of the full temporal complexity of biomass shifts is given in Fig. 6, which shows the 3-yr average position of each lake. This figure demonstrates that most lakes lie along a continuum of variation. M8, O1, and

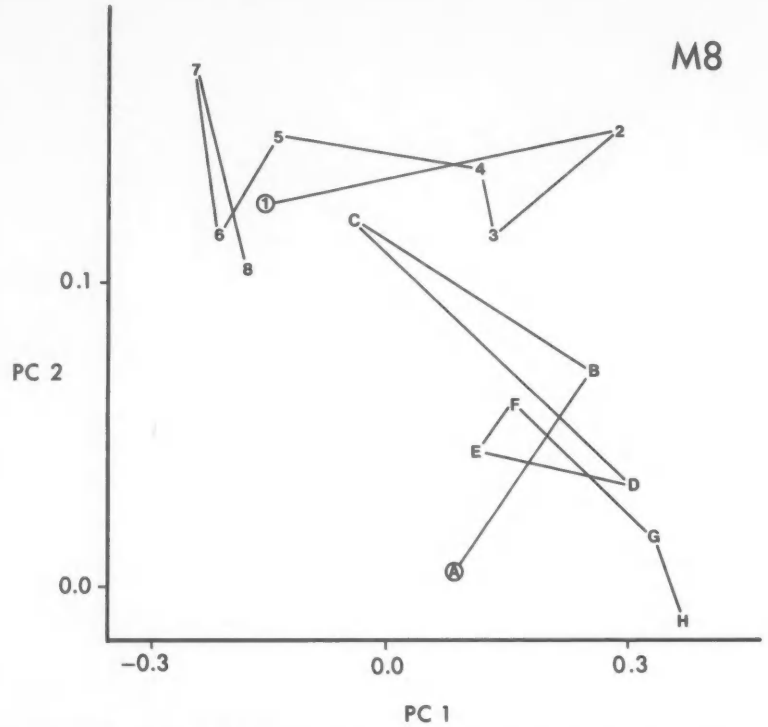

FIG. 2. Trajectories of biomass proportions in principal component space for lake M8 in 1978 and 1979. Letters increase through the sampling season for 1978, whereas numbers represent the 1979 sampling season. The first sampling period of each year is indicated by a circle.

possibly M5 appear to be outliers. M8 and O1 have unusually high planktonic biomass relative to our other lakes, whereas M5, which lies on the contact between the Precambrian Shield and Palaeozoic geologic units, is intermediate in its chemistry and again different from our other lakes.

INTERPRETATION OF COMPONENTS

Essential to the analysis of these temporal patterns in biomass fluctuation is an adequate interpretation of the meaning of the principal components. Table 3 gives the loading pattern for the analysis; it lists the correlations of each component with each of the 16 size-class variables.

Because PC 1 loads heavily on filamentous algae, we interpret it to represent primarily the proportion of filamentous algal biomass in the plankton. To test this, we regressed PC 1 against the proportion of inedible phytoplankton (variables 5 and 6 of Table 2) and found a linear relationship ($P < 0.001$) with $r = 0.995$. Thus, we feel justified in interpreting high values on PC 1 as corresponding to a high proportion of filamentous algae.

PC 2 loads highly on the two larger edible phytoplankton size classes and (with opposite sign) on the medium-sized herbivorous zooplankton class. Regression of PC 2 scores against the ratio of edible phytoplankton to herbivores gives a good fit ($P < 0.01$) to a linear relationship, but with somewhat more scatter than the PC 1 regression: here, $r = 0.730$. We interpret high values on PC 2 to represent a relatively high ratio of edible phytoplankton to herbivorous zooplankton, whereas low values represent a low ratio of the standing crop of edible algae relative to that of grazers. Because this interpretation involves the ratio of standing crops, we do not intend to imply any dynamic cause-and-effect relationship between these size classes.

INTERPRETATION OF TRAJECTORIES AND THEIR MEAN LOCATION

Our goal is to understand the role that physicochemical factors play in determining both the average position and the direction of movement between years of our lakes in principal component space. Variations among lakes in their seasonal patterns within years were so diverse that we were unable to detect common patterns. This may be because our lakes

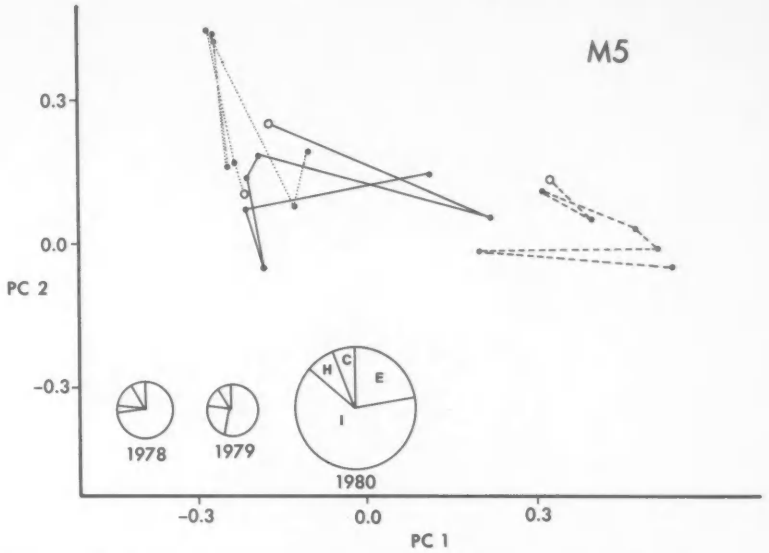

FIG. 3. Trajectories of biomass proportions in principal component space for lake M5 over three sampling seasons. Total biomass is proportional to the size of the pie chart, whereas the proportions of the four categories are indicated clockwise from 12:00 with letters (E, edible phytoplankton; I, inedible phytoplankton; H, herbivorous zooplankton; C, carnivorous zooplankton). Trajectories for each year begin with an open circle. Dotted lines indicate 1978; solid lines, 1979; dashed lines, 1980.

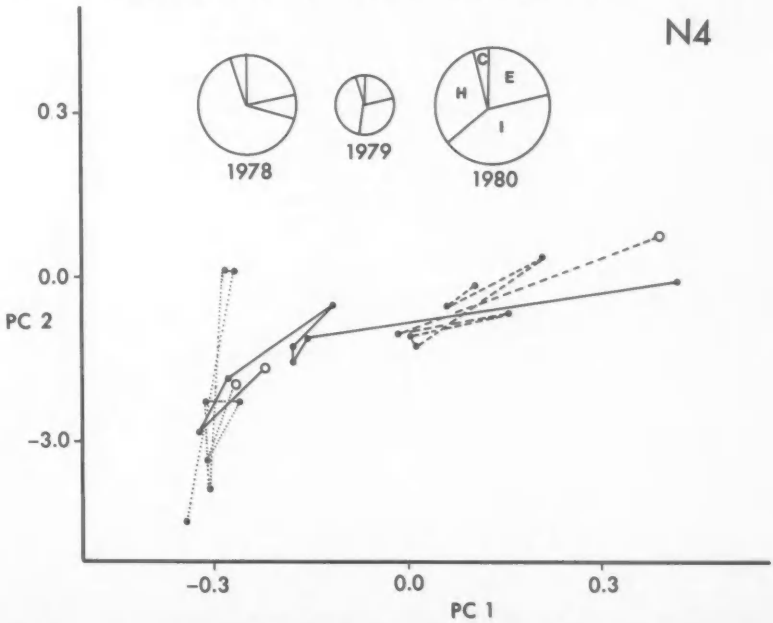

FIG. 4. Trajectories of biomass proportions in principal component space for lake N4 over three sampling seasons. Conventions as in Fig. 3.

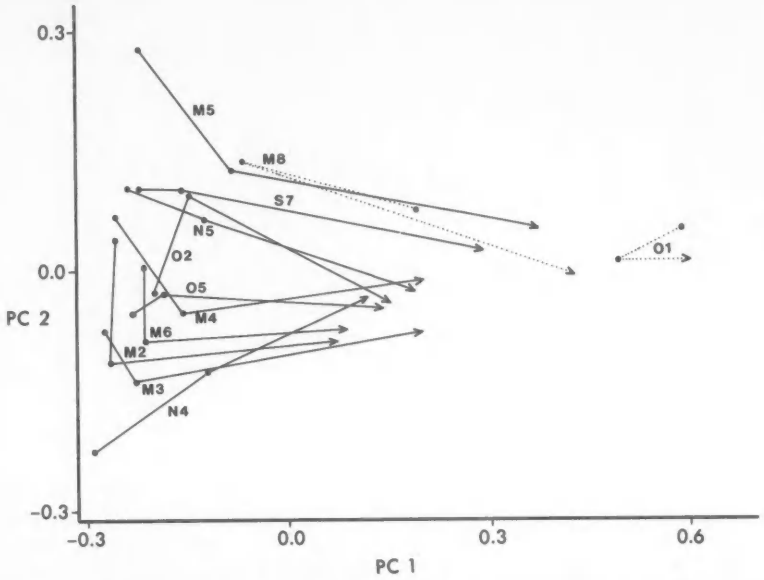

FIG. 5. Mean positions of each lake for each year in principal component space. Year 1978 is indicated with circles, whereas year 1980 is indicated with arrowheads. The two lakes that show reversals of movement are shown with dotted lines.

comprise several different lake types (Paloheimo and Zimmerman 1983). Therefore, we have focused in this paper on explaining variations among years.

One of the primary determinants of the mean position of a lake along PC 1, accounting for a least 90% of the variation (in terms of R^2) in stepwise linear regressions, is the average chemical composition of the lake with respect to measured concentrations of 13 metals and ligands (Na, K, Ca, Mg, Cl, Fe, SO_4, NO_3, Kjeldahl N, total P, Mn, organic C, inorganic C). In particular, the analytical concentrations of the conservative elements Na, K, and Cl alone explain 92% of the variation in position along PC 1.

Although mean position appears to be determined by water chemistry, the observed yearly shifts along PC 1 seem to be related to changes in mass balance of nutrients, at least as reflected in changes in total annual precipitation, where the correlation is 0.85 with PC 1. Precipitation records are based on data for each physiographic region from federal government stations, none of which are located directly on our lakes (whose region is denoted by a letter in the lake codes of Table 1).

These findings suggest that flushing rate is an important parameter controlling movement along PC 1. However, the location of our precipitation stations did not allow us to monitor the small-scale hydrologic changes which have been shown to be important in influencing mass balance of chemical constituents of lake waters at the Experimental Lakes Area (Newbury and Beaty 1980).

Newbury and Beaty's model suggests that as precipitation increases, water renewal times decrease as a nonlinear function of watershed area. However, increased precipitation may also affect rates of nutrient export from the watershed. Our data indicate increasing precipitation inputs to our systems over the 3-yr study period. If, in fact, the flushing rates correspondingly increase, then nutrient concentrations should decrease, provided that loadings remain constant. Although we find such a trend in nutrient concentrations, the decrease is not statistically significant. A recent model predicts that phytoplankton community response to lower nutrient concentrations across a set of lakes will be manifest in a downward shift in nannoplankton size structure (Paloheimo and Zimmerman 1983). Within our subset of lakes we did not find such a downward shift. We also observed an overall increase in total biomass, primarily due to an increase in the inedible fraction, which is not consistent with the classic pattern of response to decreasing nutrient concentration. These discrepancies may result simply from the restricted series of Ontario lakes which we are using. Over a larger spectrum of lakes, the general trends noted above may well hold. Four of our lakes are on metered watersheds, and precise hydrologic budgets, which are being determined, will enable us to explore this matter.

In contrast, mean position along PC 2 is determined, at least in part, by the physical structure of the lake. Lake volume alone accounts for 41% of the variance in a lake's mean position along PC 2. Because many morphometric parameters are highly correlated and are dependent both upon the geomorphology of the watershed and upon the mechanism of lake

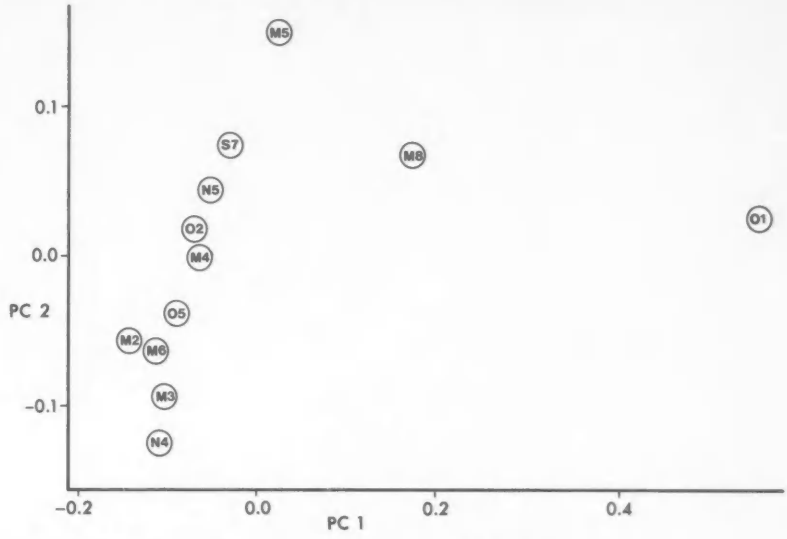

FIG. 6. Overall mean position of each lake in principal component space.

TABLE 3. Correlations of original 16 variables with principal components axes, based on the covariance matrix.

Variable	PC 1	PC 2
Edible 1	−0.00126	0.00323
Edible 2	−0.02803	0.02594
Edible 3	−0.13438	0.20397
Edible 4	−0.20088	0.74790
Inedible 1	−0.02639	−0.11154
Inedible 2	0.92040	−0.01299
Herbivore 1	−0.03682	−0.04512
Herbivore 2	−0.02568	−0.03343
Herbivore 3	−0.28853	−0.60488
Herbivore 4	−0.06826	−0.11957
Herbivore 5	−0.02751	−0.00402
Carnivore 1	−0.00437	0.00287
Carnivore 2	−0.04147	−0.04625
Carnivore 3	−0.01966	−0.01246
Carnivore 4	−0.00642	−0.00264
Carnivore 5	−0.01074	0.00899

formation (Kent and Wong 1982), we used the first principal component of six morphometric variables (mean and maximum depths, surface area, volume, perimeter, percent littoral zone area) as a summary variable. This component, which accounted for 66% of the total variation in lake morphology for a larger set of lakes (Zimmerman et al. 1983) only explained an additional 6% of the variation in a lake's mean position along our PC 2. Nevertheless, we believe that the average position of a lake along PC 2 is a reflection of its gross size and shape.

As yet, we do not know what determines movement along PC 2, that is, what influences changes in the relative proportions of edible phytoplankton and herbivorous zooplankton, as noted above. There may be, in fact, no abiotic factors responsible for biomass shifts along this component, which therefore may represent irreducible (from the perspective of this analysis) aspects of internal plankton dynamics. Alternatively, other physicochemical models (Zimmerman et al. 1983), including stratification patterns, which we have yet to apply to biomass trajectories, may prove useful.

We suggest that principal components analysis provides a useful way to handle the complexity of year-to-year changes in the allocation of biomass among planktonic compartments. We hypothesize that the relative allocation of biomass among lakes is determined, firstly, by the proportion of inedible filaments in the total planktonic biomass as a function of water chemistry, and, secondly, by the edible-phytoplankton/herbivorous-zooplankton ratio as a function of morphometry of the lake. Furthermore, we predict that changes in biomass allocation between years is determined principally by changes in nutrient concentration. Whether or not our interpretation of the meaning of the components for our set of Ontario lakes is applicable more broadly will require comparisons with similar data from other sets of lakes. The technique does provide a hypothesis-generating perspective upon the plankton dynamics of lake ecosystems. In addition, variance-weighted scores are produced which can be more useful in statistical models than the raw biomass data themselves. Indeed, our results demonstrate the advantage, in terms of explanatory power, of multivariate techniques when dealing with the complexity of plankton−environment interactions.

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Size Distribution of Pelagic Particles in Lakes[1]

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When data are grouped into logarithmically equal size intervals, the standing crop of plankton in lakes forms a bimodal distribution with the peaks centered at ~10 and 500 μm equivalent spherical diameter. This "jagged" spectrum is quite similar to marine spectra characteristic of inshore habitats and offshore surface waters at high latitudes. It is different from the "flat" spectra characteristic of the surface waters of equatorial and subtropical oceans, and of all oceans at depth. The ratio of phytoplankton/zooplankton biomass in lakes ranges from 0.04 to 597.0, with most values falling within the range of 0.5–3.33 predicted for marine pelagic communities. Particle-size theory predictions of fish standing stock in two study lakes compare quite well to the actual fish biomass measured in the lakes. In contrast to the linear relation between phytoplankton and fish stocks predicted by the theory, a curvilinear relationship exists, suggesting that overall ecosystem productivity may influence particle-size patterns. To facilitate further comparisons between marine and freshwater ecosystems, we argue that additional information on the effects of spatial heterogeneity, nonliving particulate matter, automated measurement techniques, and benthic–pelagic coupling on particle-size distributions is required.

SPRULES, W. G., J. M. CASSELMAN, AND B. J. SHUTER. 1983. Size distribution of pelagic particles in lakes. Can. J. Fish. Aquat. Sci. 40: 1761 – 1769.

Quand on groupe les données selon des intervalles de taille répartis également au moyen de logarithmes, la biomasse de planctons lacustres forme une distribution bimodale dont les sommets sont centrés à environ 10 et 500 μm de diamètre sphérique équivalent. Ce spectre « dentelé » est très semblable aux spectres marins caractéristiques des habitats côtiers et des eaux superficielles océaniques à hautes latitudes. Il est par contre différent des spectres « aplatis », caractéristiques des eaux superficielles des océans équatoriaux et subtropicaux et des eaux profondes de tous les océans. Le rapport entre la biomasse phytoplanctonique et zooplanctonique lacustre varie de 0,04 à 597,0, la plus grande partie des valeurs se trouvant dans la gamme de 0,5 à 3,33 extrapolée pour les communautés marines pélagiques. Basées sur la théorie de la taille des particules, les prédictions relatives à la biomasse de poisson dans deux lacs expérimentaux se rapprochent beaucoup de la biomasse réelle quantifiée. Contrairement à la relation linéaire entre le phytoplancton et les stocks de poisson prédit par la théorie, il existe une relation curvilinéaire, ce qui porte à croire que la productivité globale de l'écosystème peut influer sur les groupements de taille des particules. Afin de faciliter les comparaisons ultérieures entre les écosystèmes d'eau douce et d'eau salée, les auteurs maintiennent qu'il est nécessaire de recueillir des données supplémentaires sur l'incidence de l'hétérogénéité spatiale, des particules inanimées, des techniques automatisées de quantification et de l'association benthique-pélagique sur les distributions de taille des particules.

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IN marine pelagic ecosystems the standing crop of particulate matter (in $\mu L \cdot L^{-1}$) is relatively uniform over six orders of magnitude of particle size when data are grouped into logarithmically equal size intervals (Sheldon et al. 1972). There is only a slight decrease in concentration with increasing particle size. In practical terms this means that the biomass of bacteria

in the open ocean is roughly that of whales, or at most two to four times greater. Recognition of this regularity in the structure of marine ecosystems, and subsequent development of an underlying theory (Kerr 1974; Sheldon et al. 1977; Platt and Denman 1977, 1978; Silvert and Platt 1980) have been important contributions in the search for generalizations in ecology. It is now possible to estimate, from data on the standing stock at any size range, the standing stock (or production if size-specific growth rates are known) at any other size (Sheldon et al. 1977; Borgmann 1982).

Size relationships in marine systems result, theoretically, from a set of basic conditions that characterize this environment (Sheldon et al. 1973). The open ocean is approximately at steady state over moderate time periods; most of the primary production is by microscopic plants; each predator engulfs its smaller prey whole; the predator/prey size ratio is reasonably uniform throughout the food chain; and, at any link in the food chain, the predator/prey ratio of instantaneous productivity rates is inversely related to the ecological efficiency. This last feature derives from the dependency of physiological processes such as growth and metabolism on organism weight (Kerr 1974).

As a first approximation, these characteristics are shared by the environment and biota of the pelagic zone of lakes. Thus particle-size theory should provide a general framework for the analysis of size-dependent regularities in lake as well as marine ecosystems. The predictive capabilities of the model could be used in lake studies, and the model could provide a framework for comparisons of pelagic processes in oceans and lakes.

Our objective was to determine the extent to which particle-size distributions and standing-stock ratios in small inland lakes are similar to those for oceans. We test the applicability of particle-size theory to lakes by comparing predictions of fish biomass based on this theory to independent empirical estimates.

Methods

The 37 study lakes are located within the region of central Ontario bounded approximately by 46°45′ and 44°35′N, and 81°30′ and 78°20′W. They vary in morphometric and chemical features (Table 1) as well as in bedrock geology, cottage development, and acid loading.

Integrated epilimnetic phytoplankton samples were collected at a point of maximum lake depth from the surface to 4 m with a length of 9.5-mm-diameter tygon tubing. A 100-mL subsample was preserved in acid Lugol's iodine solution and a 5-mL aliquot placed for 24 h in a settling chamber. The settled algae were examined using phase-contrast microscopy. Cell volume was calculated by approximation to a sphere or cylinder for regularly shaped unicellular species, or from more complex geometric solids for the larger, more irregular, unicellular species. The volume of a colony was calculated as the sum of the volumes of its constituent cells, and volumes of filaments were taken as the product of filament length by (circular) cross-sectional area. Presuming a specific gravity of unity, biomasses of all cells, colonies, and filaments were derived from these calculated biovolumes.

Zooplankton samples were collected at the point of maximum lake depth by drawing a tow net from bottom to surface. The net comprised two 30-cm hoops separated by nonfiltering material, with a tapering mesh of 110 μm suspended from the lower hoop. A 12.5-cm cylindrical flowmeter was fixed between the two hoops. Animals were preserved in buffered formalin and enumerated under a dissecting microscope using a microcomputer-based measuring device (Sprules et al. 1981). Organisms were classed as herbivorous or carnivorous and their total lengths measured. Wet weights were calculated from published length–weight formulae (Hillbricht-Ilkowska and Patalas 1967; Rosen 1981).

TABLE 1. Physical and chemical properties of study lakes.

Character	Minimum	Median	Maximum
Mean depth (m)	0.9	7.8	20.1
Surface area (ha)	29.1	149.4	1142.2
Drainage area (km^2)	1.5	15.3	340.6
Flushing rate (yr^{-1})	0.11	0.52	38.40
Conductivity ($S \cdot cm^{-1}$)[a]	10	30	210
pH[a]	4.6	6.8	8.8
Total phosphorus ($\mu g \cdot L^{-1}$)[b]	0.5	4.0	27.0

[a]Taken at mid-epilimnion depth in August.
[b]Surface determination, July–August.

In 1978 the 37 lakes were visited roughly every 2 wk beginning in early May. For the analysis presented here we used the plankton data collected on the seven sampling "cycles" running from late May to late August or early September. These same seven cycles were used for the 26-, 14-, and 9-lake subsets sampled in 1979, 1980, and 1981, respectively. For a particular lake in any given year there are thus seven phytoplankton and seven zooplankton samples. Data from these samples were either statistically averaged over the season or treated individually as the analyses demanded. The one exception is for 1979 when, in addition to the regular plankton counts, enumerations of "pooled" samples were done. These pooled samples were created for a given lake for both phyto- and zoo-plankton by removing aliquots from each of the seven individual samples and combining them. The biomass spectra presented below are based on these pooled samples.

Fish biomass data are based on samples collected in the summers of 1979 and 1980. Each lake was intensively sampled once during this period with gill nets and trap nets of various mesh sizes, and with baited minnow traps. A triple-beam balance was used in the field to obtain fresh fish weights. A quantitative electrofishing survey was conducted on a subset of nine lakes during September and October 1981, using a boat-mounted boom shocker (Smith-Root SR18) delivering from 2.5 to 5.5 A when operated at 600–1000 V. Transects 2 or 3 m wide were fished in the nearshore area at night at three to seven separate locations for total lengths per lake ranging from 604 to 2234 m, depending on lake size. Fish were either weighed at time of capture or were fixed in 10% formalin, preserved in 70% alcohol, and subsequently weighed on an electronic balance. Total fish catch was converted to aerial biomass concentration using these weights.

All statistical analyses were done at the University of Toronto computing centre using the Statistical Analysis System (SAS) (Helwig and Council 1979).

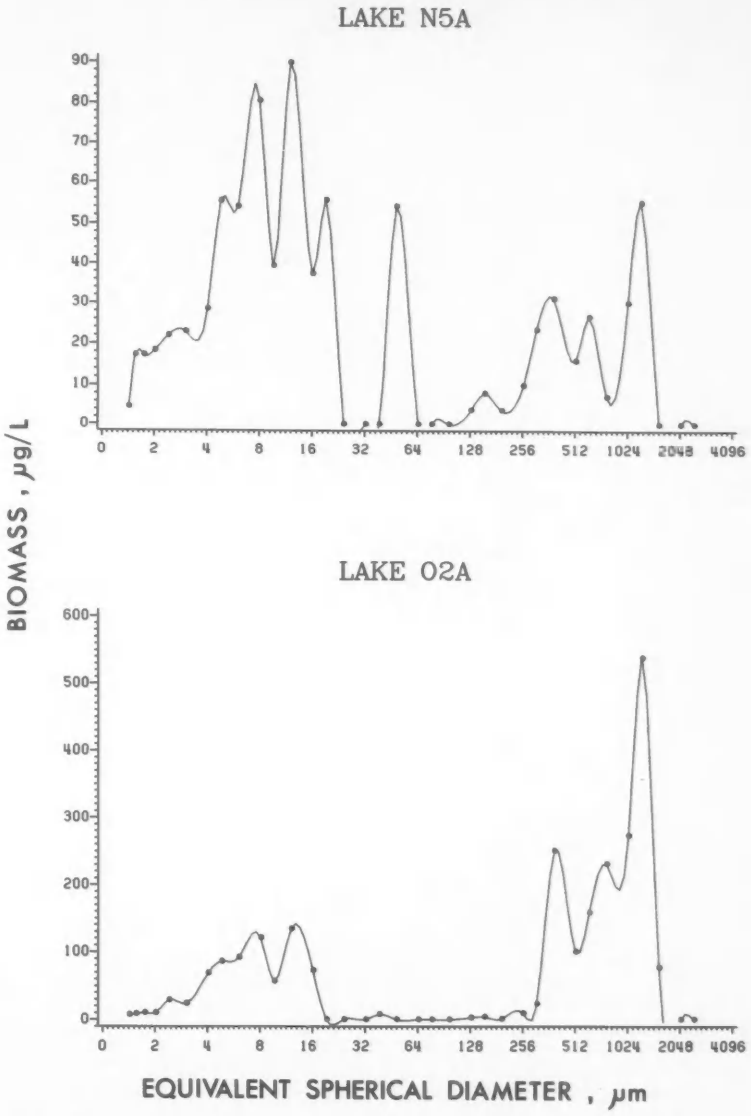

FIG. 1. Particle-size distributions for selected lakes. Lake codes are indicated on each panel. Note different scales on Y-axis.

Results and Discussion

SPECTRUM SHAPE

Sheldon et al. (1972) used a Coulter counter to enumerate small particles in the ocean. The equivalent spherical diameters thus measured for each particle were then grouped into $\log_2$ size classes with concentration expressed as $\mu L \cdot L^{-1}$. We have expressed the size of each planktonic organism as the diameter of a sphere which has the same volume (phytoplankton) or weight (zooplankton) and grouped them into $\log_2$ size classes. We have measured biomass in $\mu g \cdot L^{-1}$, which is effectively the same as $\mu L \cdot L^{-1}$ because the specific gravity of planktonic organisms is so close to unity. Although not

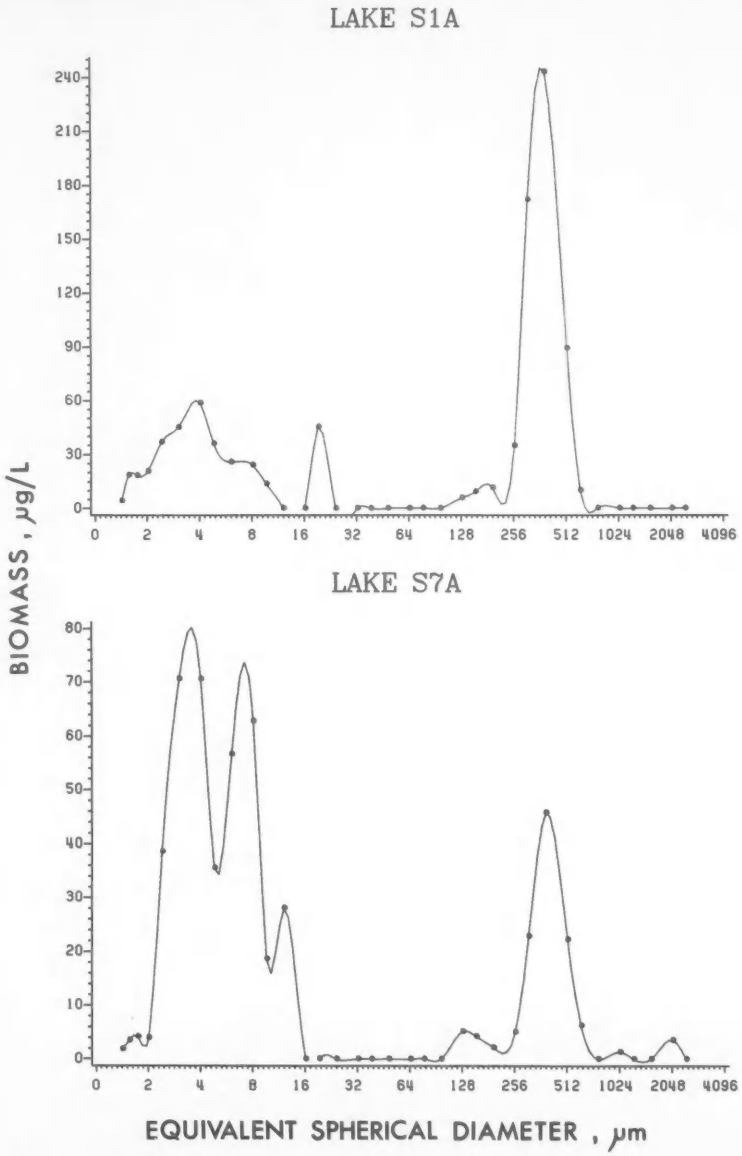

FIG. 2. Particle-size distributions for selected lakes (designations as in Fig. 1).

identical, these two methods of particle characterization are sufficiently similar for the general comparisons we make here (P. Schwinghamer, R. W. Sheldon, and S. R. Kerr, 1983, unpublished data; R. W. Sheldon, Bedford Institute of Oceanography, personal communication).

Plankton size-spectra based on the 1979 pooled samples vary in shape from those in which the phytoplankton peak (~1–70 µm equivalent spherical diameter, ESD) is only slightly larger than the zooplankton peak (roughly >200 µm ESD) to those in which one peak clearly predominates (Fig. 1 and 2). In these spectra, particles up to about 16 µm ESD comprise mainly unicellular algae and bacteria whereas

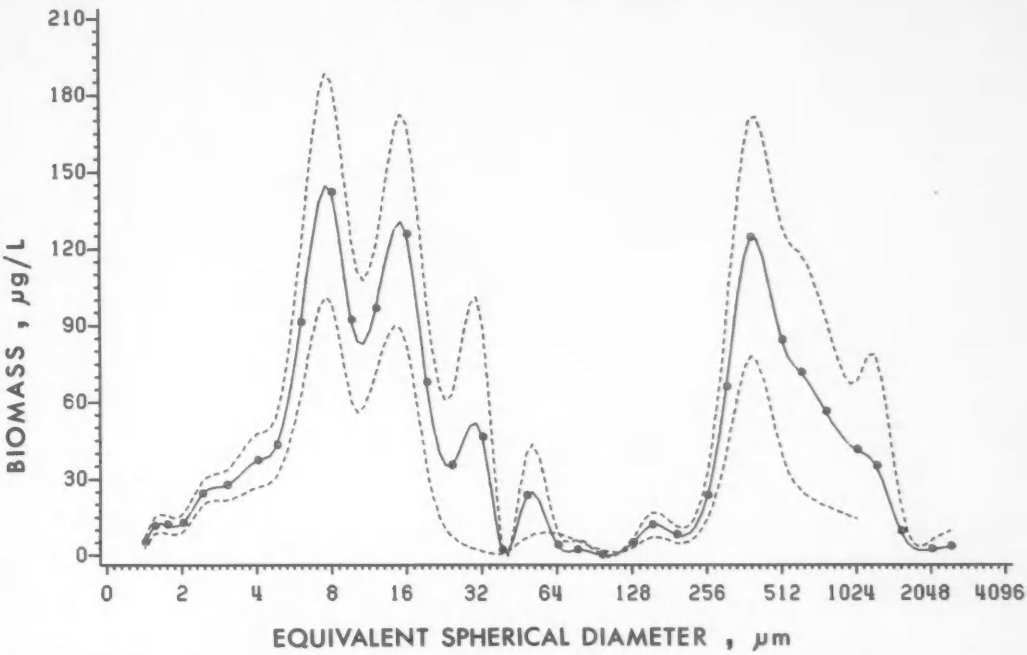

FIG. 3. Average particle-size distribution calculated from individual distributions for 26 lakes. Ninety-five percent confidence interval is shown.

the remainder up to about 70 µm ESD comprise larger unicellular algae and colonial and filamentous forms. In the zooplankton peak the smallest particles are rotifers and copepod nauplii, those in the middle are cladoceran and calanoid grazers and cyclopoid copepods, and the largest are predatory calanoids, *Chaoborus* and *Leptodora*. For instance, in lake N5A there is a large population of filamentous algae centered at 64 µm whereas in lake O2A there is a peak of large *Daphnia* at 1300 µm (Fig. 1). These spectra thus summarize a considerable amount of information about the size distribution of plankton in lakes and illustrate the degree of variation among lakes. Ongoing analyses are designed to relate this variation to other characteristics of lakes. For instance in the acid-stressed Sudbury lakes (S1A and S7A, Fig. 2) the shift to smaller sizes in the phytoplankton peak is consistent with the general pattern of reduced size in stressed communities (Kerr 1974).

This variation in plankton size-distribution among lakes can be summarized by averaging the individual spectra for all 26 lakes (Fig. 3). It is clear that, over a considerable range of lake types, the plankton size spectrum is characterized by two distinct peaks centered at roughly 10 and 500 µm ESD, corresponding, respectively, to phytoplankton and zooplankton. Three regions of low biomass occur at ~1, 100, and 2000 µm ESD. Because of the rigor of our sampling and enumeration techniques, we judge these troughs not to be artifactual, although we are currently evaluating biomass in these regions more intensively. For instance, the trough at 100 µm lies between large algae and small rotifers. Planktonic ciliates could contribute biomass here, but such data for our lakes (M. Gates, University of Toronto, Toronto, Ont. personal communication) indicate that these organisms make up a very modest fraction of the wet weight of plankton which falls in the 50- to 70-µm range, i.e. on the shoulder of the phytoplankton peak. The trough at 2000 µm lies between the large invertebrate predators, such as *Chaoborus* larvae and *Mysis*, and the larval fish, which would fall into some larger size category. At the other extreme of the size scale, around 0–2 µm, small algae and bacteria contribute comparatively minor amounts of biomass.

These three regions of relatively low biomass below, above, and between the phytoplankton and zooplankton peaks imply that there are certain limitations to the physical size attainable by planktonic organisms in freshwater. Presumably there are structural limits to the maximum size of algae; in fact, the largest species reported from either marine or freshwater ecosystems correspond roughly to the 65-µm upper boundary of the phytoplankton peak. The minimum size of herbivorous zooplankters must be determined, at least partly, by physical features of the grazing process. A typical aquatic herbivore is roughly 20–30 times the size of its prey (Sheldon et al. 1977), suggesting that a grazer feeding on the 8-µm particles at the mode of the phytoplankton peak (Fig. 3) should be at least 160–240 µm ESD, i.e. roughly at the left-hand tail of the zooplankton peak. Smaller grazers relying on the comparatively low biomass of smaller algae would

TABLE 2. Phytoplankton/zooplankton biomass ratios for all sampling cycles in all lakes, 1978, 1979, 1980 (sample size = 602).

Quantiles, %	Ratio
Maximum	594.00
99	144.50
95	16.40
90	7.85
75	3.52
50 (median)	1.64
25	0.77
10	0.40
5	0.32
1	0.16
Minimum	0.04

be correspondingly rare. Strickler (1983) suggests that zooplankton grazers must reach a certain minimum size to overcome the hydrodynamic forces in their highly viscous environment.

A number of important points emerge from comparisons of our data on size spectra with those from oceans and other lakes. The only other particle-size data for temperate lakes of which we are aware are presented as parts of zooplankton grazing studies for Lake Michigan (Vanderploeg 1981) and for Green Bay, Lake Michigan and Lake Winnebago, Wisconsin (Richman et al. 1980). These data are for small particles only (up to 30–50 μm ESD), and both studies show one main biomass peak centered at roughly 10–15 μm, with low biomass on either side of the peak. Similarly, for our study lakes most of the small particle biomass is centered at 11–12 μm (left-hand peak, Fig. 3). This suggests that there is some regularity in the size distribution of small particles in lakes. The Coulter counter used in the grazing studies processes both living and nonliving particles, whereas our semiautomated procedures process only living organisms. Nevertheless, the particle-size spectra are quite similar, suggesting that spectral shape is not particularly sensitive to these differences in technique. Furthermore, the troughs we have observed on either side of the phytoplankton peak are confirmed by these Coulter data. As far as we are aware, no freshwater size distributions for particles larger than 50 μm have been published.

Most of the available marine distributions are also for small particles, although there are some which include larger particles up to about 2000 μm ESD. The single biomass peak of small particles which characterizes lake spectra (Fig. 3) is also typical of surface samples from polar and temperate oceans (Sheldon et al. 1972), although the latter are centered further along the size axis at ~20 μm. The complete plankton spectrum from a temperate ocean surface sample, and those from inshore marine areas, are bimodal, or jagged, like the mean spectrum for lakes (P. Schwinghamer, R. W. Sheldon, and S. R. Kerr, 1983, unpublished data). On the other hand, marine spectra for plankton particles of all sizes from the surface of subtropical and equatorial oceans, and from depth at all ocean sites sampled, tend to be much "flatter," i.e. with roughly equal biomass in all size categories (Sheldon et al. 1972, 1977). Thus the peaked nature of the particle-size spectrum for lakes is most similar to marine spectra from surface waters at high latitudes and from inshore areas. Seasonal variability tends to be high in these marine areas as well as in lakes, and it could be that jagged particle-size spectra are typical of such habitats. Seasonal variability is presumably less in lower latitude oceans and at depth in all oceans. These sites are characterized by flat spectra. As argued above, the fact that the Coulter counter was used to generate the marine data should not seriously affect these comparisons.

TABLE 3. Phytoplankton/fish biomass ratios for two lakes.

Lake	Biomass ($\mu g \cdot L^{-1}$) Phytoplankton (A)	Fish (B)	Ratio (A/B)	Adjacent trophic level ratio $(A/B)^{0.5}$
Crosson	512	620	0.83	0.9
Plastic	615	121	5.1	2.3

BIOMASS RATIOS

Another general feature of limnetic plankton communities indicated by the mean-size spectrum is the only slightly greater standing stock of phytoplankton compared to zooplankton (Fig. 3). To obtain a more precise evaluation of this pattern, we computed the ratio of phytoplankton/zooplankton biomass for each lake on each sampling cycle for 1978–80 (Table 2). There is clearly tremendous variation in this ratio, ranging from a minimum of 0.04 in an oligotrophic lake with high zooplankton densities following the spring algal bloom, to a maximum of 597.0 in a small, shallow lake containing an enormous population of filamentous algae. These variations reflect seasonal cycles of phytoplankton and zooplankton abundance as well as structural differences in plankton communities among lakes. The median value of the ratio is 1.63 and 70% of the values fall between roughly 0.3 and 3.5 (Table 2). For comparison, Kerr (1974) predicts that the biomass of a trophic level should be roughly 1.2 times that of its predator, whereas Sheldon et al. (1972) expect a value of unity or slightly greater. In a more detailed analysis Sheldon et al. (1977) determined that, for ecologically realistic ranges of predator/prey size ratios and predator population growth efficiencies, prey/predator standing stock ratios could be expected from about 0.5 to 3.3.

Other comparable data for lakes are few, but reanalysis of McCauley and Kalff's (1981) regression between phytoplankton and zooplankton standing stock for 17 temperate lakes from North America and Europe ranging over a considerable trophic gradient produces phytoplankton/zooplankton biomass ratios of 0.6–2.5. This range conforms closely to the values predicted by Sheldon et al. (1977) and to most values noted here. Although not strictly comparable, Peters (1983) presents data on the phosphorus content of lake plankton that give ratios in adjacent $\log_{10}$ size classes of 1.0–1.2. Some tropical lakes follow the observed patterns in biomass ratios, but others have very high ratios (Hecky 1983), particularly those in which the phytoplankton community is dominated by blue-green algae. Similarly, those of the lakes discussed here which have unusually high ratios (i.e. above roughly 20 and

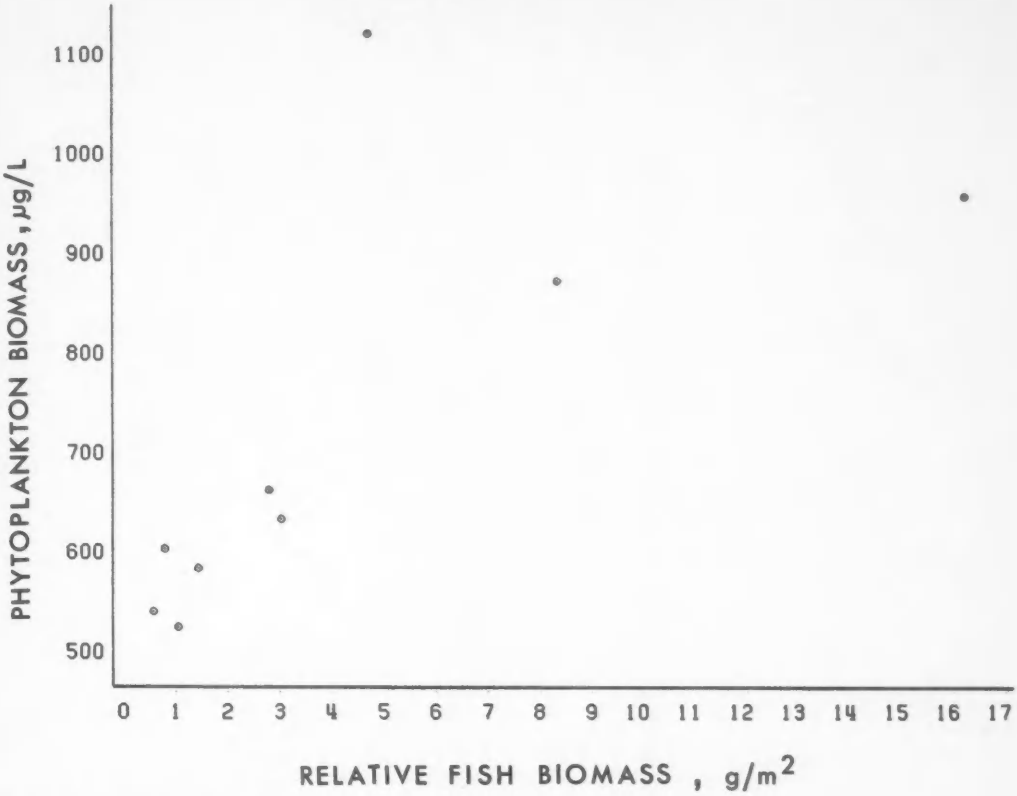

FIG. 4. Relation between phytoplankton biomass and fish catch per unit effort.

up to 594) generally contain relatively high densities of blue-green filamentous algae, a food resource not assimilated by most zooplankton grazers (Webster and Peters 1978).

It thus appears as if prey/predator biomass ratios in lakes fall within the theoretical limits determined for oceans, at least for planktonic organisms up to 2000 µm ESD. Our median value of 1.6 for lakes is slightly higher than the value of 1−1.2 predicted for oceans. Whether this difference is real or apparent cannot be resolved until a more detailed breakdown of the marine data is attempted. Unfortunately the marine data have been insufficiently analyzed to determine how much spatial and temporal variation there is in standing stock ratios.

FISH BIOMASS PREDICTIONS

Because these patterns in plankton biomass ratios in lakes fit the particle-size model reasonably well, it is of interest to extend the model to fish, the next major size class of particles in lakes. Because phytoplankton are more uniformly distributed in the epilimnion from which they were sampled than are zooplankton over the whole water column, we consider the phytoplankton data to be less prone to sampling error. We will thus use phytoplankton data to estimate fish biomass. On the basis of a median biomass ratio between adjacent plankton trophic levels of about 1.6 (Table 2), fish biomass is expected to be roughly 1.6^2, or 2.6 times the phytoplankton biomass. Exhaustive mark/recapture estimates of the total population of all major fish species were available for two of the lakes (Harvey and Lee 1981). On the basis of these total numbers, and mean fresh weights of the fish, it was possible to calculate the total biomass of fish per unit volume of the oxygenated stratum of each lake. These were compared with the mean annual phytoplankton biomass in the lakes for the same year (Table 3) and indicate adjacent trophic level ratios of 0.91 and 2.3. The ratios for both lakes are within the ranges predicted by Sheldon et al. (1977), and the mean value (1.65) is essentially the same as the median value of 1.6 calculated from the plankton data.

The electrofishing survey data from nine of the lakes provide a second means of comparing the relative sizes of plankton and fish stocks (Fig. 4). The phytoplankton data are mean epilimnetic biomasses for 1981 whereas the fish data are standardized nighttime catches along nearshore (0.75−2.3 m lake depth) transects. Because the transect depths were so uniform, the expression of fish biomass concentration on an

areal basis differs by only a constant from a volumetric basis. On the basis of the relatively uniform standing-stock ratios predicted by particle-size theory, one would expect a linear relationship between the sizes of the plankton and fish stocks. The relation is monotonic and increasing but not quite linear (Fig. 4). There is one outlying lake which has high densities of filamentous algae, a food base which typically supports a low biomass of zooplankton and hence of planktivorous fish. The data in fact suggest a decreasing phytoplankton/fish biomass ratio with increasing fish biomass. This is precisely the trend observed by Gascon and Leggett (1977) in Lake Memphremagog (Quebec−Vermont) — an increase of phytoplankton biomass from the less-productive end of the lake to the more-productive end of only 1.6 times but an increase of littoral fish biomass of 3 times.

Thus, although the mark/recapture data indicate that ratios of phytoplankton/fish biomass fall within the range predicted by particle-size theory, the electrofishing results suggest that the actual value of the ratio within this range may depend upon ecosystem productivity. This, in fact, is also suggested by the data of McCauley and Kalff (1980), as their range of 0.6−2.5 in the phytoplankton/zooplankton biomass ratios corresponds to a range of 427−10 889 $\mu g \cdot L^{-1}$ in phytoplankton biomass. We have summarized a variety of other data, including some plankton data from the lakes in this study, that indicate a similar dependency of biomass ratios on other ecosystem characteristics, particularly productivity (Sprules and Knoechel 1983). Again, insufficient data are available to determine whether there is a similar relationship in oceans.

General Discussion

Although there are clearly similarities in the particle-size spectra of lakes and oceans, some important differences remain. In terms of biomass ratios of adjacent trophic levels, the patterns in lakes and oceans are similar. For oceans these ratios are predicted to vary from roughly 0.5 to 3.3 with a median value of 1.0 to 1.2. In lakes most values of the ratio fall between 0.3 and 3.5 with a slightly higher median value of 1.6. This correspondence is rather high in view of the emphasis on theory and "interpretive summaries" (Sheldon et al. 1972) in the marine data versus the dependence on empirical observation and statistical detail in the freshwater data. Because the general theory of particle-size distribution makes specific predictions about biomass ratios, not spectral shape, the correspondence is particularly significant. The features of the ecosystem underlying the general theory of biomass distribution, i.e. predator/prey body size ratios, weight-dependent physiological processes, and the inverse relation between ecological efficiency and particle productivity, must therefore be equally characteristic of lakes and oceans. Thus techniques for predicting standing crop and production should be common to these two major ecosystems, as was verified by our use of the theory to predict fish biomass from phytoplankton data in lakes.

On the other hand, the shape of the plankton size-spectrum was not consistent between oceans and lakes. The freshwater spectrum is generally jagged, with two distinct peaks separated by a trough. This is most similar to ocean spectra characteristic of offshore surface waters at polar and temperate latitudes, as well as of inshore localities. By contrast, ocean spectra from lower latitudes, and at depth, tend to be flat with roughly equal biomass in all size intervals. It is these latter spectra which have led to the generalization that all ocean particle-size spectra are flat (Sheldon et al. 1972, 1977). We have speculated that it is the seasonally variable nature of temperate lakes, and of high latitude oceans, that underlie their common, jagged size-spectra. Inshore marine habitats are also likely to be temporally variable. On the other hand oceans at depth and lower latitude oceans are likely to be more stable. Mechanisms which underlie this hypothesized relationship between temporal variability and spectrum shape have currently not been resolved.

Although there thus appears to be general utility in the theory of particle-size distribution, there are certain key elements of the approach which require refinement. Differences in data treatment preclude anything other than the general comparisons made above between lakes and oceans. For instance, Sheldon et al. (1972) illustrated general patterns by choosing individual spectra subjectively judged to be representative, rather than by statistically averaging their data as we have done. Such detail of analysis is required to verify the perceived geographic trends in the shape of marine spectra, and their peakedness in certain localities. It would also be useful to have detailed calculations of adjacent trophic level biomass ratios from marine samples, not only for comparison with those we have generated for lakes (Table 2), but also to provide an exact, numerical evaluation of the subjectively determined ratio of roughly 1:1 (Sheldon et al. 1972). More exact calculations of the sort we have presented are required before subjectively determined generalizations become too firmly ensconced as general theory.

We also emphasize that there are fundamental differences in the techniques used to generate marine and freshwater spectra. The former were generated from automated Coulter counts whereas the latter were based on direct visual counts. Not the least of the resulting differences in data is the differential emphasis on nonliving particles. Although we have shown that spectral shape appears to be relatively insensitive to technique, further confirmation of this is required. Given that the general theory is based on trophic interactions between particles, it is unclear exactly how nonliving particles should be treated. These particles can be consumed by some grazers and can also become substrate for bacteria.

One of the major features of particle-size spectra that emerges upon examination of either marine or freshwater data is their tremendous temporal and spatial variability. This is not new to any ecologist, nor does it detract from the utility of the general theory, but rather should stimulate use of the theory for analysis of this structural variation in aquatic communities. In particular, we have raised the notion that patterns in the shape of size spectra, and in the magnitude of biomass ratios, may only be apparent within a suitably homogeneous set of habitats. For instance, there is evidence that patterns in phytoplankton/zooplankton and phytoplankton/fish biomass ratios are dependent on system productivity. Now that some general trends have been established, it is clearly necessary to begin detailed analyses of variation in particle-size spectra. W. Silvert (Bedford Institute of Oceanography, Halifax, N.S.,

personal communication) points out that to do so one must develop a means of quantifying the varying shapes of particle-size spectra. He suggests that some techniques of spectral analysis may be profitably applied to the development of a single index containing information on both the height of biomass peaks and their location on the size axis.

Finally, the particle-size approach discussed here can clearly be extended beyond the pelagic zone to other aquatic habitats. To this end Schwinghamer (1981) has presented some particle-size spectra for marine benthic communities. His statistically averaged spectrum for benthos can be compared to ours for plankton. Intriguingly, the two troughs and three peaks of the marine benthic spectrum coincide with the three troughs and two peaks of the freshwater pelagic spectrum; in other words the two spectra are inverse images of one another. Schwinghamer et al. (1983, unpublished data) speculate that this relationship results from trophic coupling between pelagic and benthic communities. If this hypothesis is correct, we should observe even stronger relations between benthic and pelagic communities in lakes than oceans, because the smaller size of lakes should allow benthic and littoral influences on pelagic communities to be stronger than in oceans (L. B. Holtby, Pacific Biological Station, personal communication).

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Size Structure of the Plankton Community Along the Trophic Gradient of Lake Memphremagog[1,2]

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PETERS, R. H. 1983. Size structure of the plankton community along the trophic gradient of Lake Memphremagog. Can. J. Fish. Aquat. Sci. 40: 1770 – 1778.

The size distribution of epilimnetic plankton at four sites of differing trophic state was examined from May 1977 to May 1978 to examine the applicability to lakes of Sheldon's hypothesis that logarithmically ordered size classes contain approximately constant concentrations of biomass. The plankton was sized by serial filtration through a series of screens of mesh size 102, 75, 55, 35, 20, and 10 μm and a 0.45-μm Millipore filter. Biomass in each fraction was measured as particulate phosphorus concentration. I tested the hypothesis by examining the fit of regressions of particulate P concentration in each sequential fraction against the logarithm of the geometric mean of the meshes used to delimit that fraction. Sheldon's hypothesis leads one to expect a linear relationship. In most cases this was found but exceptions were common, and some size classes contained significantly more or less P than the linear model (Sheldon's hypothesis) would suggest. Comparison of the amount of P in the size classes I studied with previous estimates of the biomass of zooplankton and fish suggest that larger organisms may also fit the relation. The slope and intercept of these regressions between biomass and filter size increase with lake trophic state. This may allow an approximate prediction of community size structure in other lakes based on measured or predicted concentrations of total phosphorus.

PETERS, R. H. 1983. Size structure of the plankton community along the trophic gradient of Lake Memphremagog. Can. J. Fish. Aquat. Sci. 40: 1770 – 1778.

La distribution par taille du plancton épilimnétique à quatre sites de conditions trophiques différentes a été étudiée entre mai 1977 et mai 1978 afin de vérifier l'application à des lacs de l'hypothèse de Sheldon voulant que des groupes de taille disposés logarithmiquement contiennent des concentrations de biomasse approximativement constantes. Le plancton a été séparé par taille à l'aide de filtration en série à travers des tamis de grandeurs de maille de 102, 75, 55, 35, 20 et 10 μm, et un filtre Millipore de 0,45 μm. Dans chaque fraction, la biomasse a été mesurée comme concentration de phosphore particulaire. Pour vérifier l'hypothèse, j'ai examiné l'ajustement des régressions de la concentration de P particulaire dans chacune des fractions de la série contre le logarithme de la moyenne géométrique des mailles utilisées pour délimiter cette fraction. Selon l'hypothèse de Sheldon, on s'attend à une relation linéaire. C'est bien ce qui se produit dans la majorité des cas, mais les exceptions sont communes, et certaines classes de taille contiennent significativement plus ou moins de P que le modèle linéaire (hypothèse de Sheldon) ne le laisserait supposer. Une comparaison de la quantité de P parmi les classes d'âge étudiées avec des estimations antérieures de biomasse de zooplancton et de poisson donne à penser que la relation tient également avec des organismes de plus grande taille. La pente et l'ordonnée à l'origine de ces régressions entre la biomasse et la grandeur des filtres augmentent en fonction de l'état trophique du lac. Ceci peut donc permettre de prédire approximativement la structure par taille des communautés d'autres lacs, fondée sur les concentrations mesurées ou prédites de phosphore total.

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INDIVIDUAL size and community size structure are increasingly seen as prime descriptors in aquatic biology (Kalff 1972; Pavoni 1963; Rodhe 1958; Schwinghamer 1981). For the organism, size is a major determinant of ingestion (Cammen 1980; Ikeda 1977; Nival and Nival 1976), respiration (Banse 1976; Hemmingsen 1960; Robinson et al. 1983), production (Banse and Mosher 1980; Båmstedt and Skjoldal 1980), and reproduction (Blueweiss et al. 1978).

In brief, an organism's size influences virtually all aspects of its energy and material flow (Peters 1983). At the community level, size structure plays a major role in nutrient competition (Eppley et al. 1969; Smith 1981), resource availability and use (Gliwicz 1980), and predator–prey relations (Kerr 1974). Several authors have explored the nature of community models based at least partly on size (Cousins 1980; Griesbach et al. 1982; Isaacs 1973; Sheldon et al. 1977). This approach is especially apt in planktonic systems because the organisms can easily be separated from their medium and classed according to size.

A basic element in this approach is the application of relations between individual size and function to community processes and problems. Available allometric relations predict only average values for an average organism of a given size. The large amount of residual variation around all body size relations precludes precise prediction in individual cases. However, if multispecific size classes are considered, the appropriate measure of error is the much smaller confidence region around the mean relation. An adequate description of community size structure should therefore permit more effective application of allometric relations describing biological rates.

Sheldon et al. (1972) offer the basic model for the size structure of aquatic communities ("Sheldon's hypothesis"). They proposed that, if organisms are ordered in logarithmically increasing size classes (i.e. as 1–2, 2–4, 4–8 . . . or in any other geometrically increasing sequence), then the biomass in each class would be roughly constant. There is little information to test the applicability of this model to limnetic systems and several proposals suggest that it may not apply. The proportion of nannoplanktonic algae decreases with eutrophy (Pavoni 1963; Watson and Kalff 1981) but this may be offset by increases in the bacterioplankton (Gliwicz 1969) and decreases in the average size of zooplankton (Gliwicz 1980) in richer lakes. Odum (1969) states that average size increases with succession, and Porter (1977) suggests that this may also hold in the seasonal succession of phytoplankton communities. A more explicit examination of Sheldon's hypothesis with respect to lakes is required.

Analysis of size distribution presupposes a means of sizing organisms and a method of measuring their biomass. Some techniques, like Coulter counting, image analysis or microscopy, combine both steps in a simultaneous operation. Alternatively, the plankton may be physically fractionated and the amount of biomass in each fraction subsequently measured. This approach is more tedious than electronic analysis, and fractionation by screens is not the most effective method of accurately sizing the plankton (Sheldon and Sutcliffe 1969; Sheldon 1972; Runge and Ohman 1982). However, physical separation offers the possibility of further analysis of the characteristics of each class. I chose the latter approach because the technique is to be applied in an ongoing study of the bioaccumulation of toxicants in different size classes (Griesbach et al. 1982). Samples were therefore fractionated by filtration through a graded series of screens and filters.

Biomass in each size fraction may be estimated in a variety of ways, none of which is totally satisfactory. Carbon content and dry weight might be used but these include large amounts of nonliving material. A similar reservation applies to "biovolume" estimates from the Coulter counter. Measurement of ATP concentration is the current method of choice (Holm-Hanson and Paerl 1972). Unfortunately, ATP analyses are relatively cumbersome and expensive. Instead, I used the particulate phosphorus concentration in different size classes as a measure of biomass. Phosphorus was selected because it is the biological constituent which this laboratory can measure most easily at low concentrations. In addition, once fractionated, P concentration in different size classes does not change and large numbers of analyses can be handled routinely. Phosphorus may be an appropriate approximation of biomass because it forms a relatively constant proportion of living tissue (Bowen 1979; Peters 1975). Vinogradov's (1953) extensive tabulations of the P content of 76 aquatic taxa give a mean P content of 1.15% dry weight (SD = 0.76, median = 1.02). His data also indicate some moderate differences among algae ($\bar{x}$ = 0.69, SD = 0.32, n = 27, median = 0.65), crustaceans ($\bar{x}$ = 1.10, SD = 0.59, n = 24, median = 1.04), and fish ($\bar{x}$ = 1.71, SD = 0.90, n = 25, median = 1.58) and a considerable range within each group (0.24–1.63, 0.33–2.96, and 0.66–3.10, respectively). However, P content of planktonic size classes is likely less variable than Vinogradov's lists might suggest because size classes average across taxa. Phosphorus leaches rapidly from killed plankton (Golterman 1964; Krause 1964) so that biological detritus is less likely to confound the analyses. Phosphorus carries the disadvantage that some inorganic particulates will be measured as biomass and that some colloidal P will be analyzed with the smallest size class. I know of no estimate of the latter artifact. Killed samples from the central basin of Lake Memphremagog leached 87% of all particulate P within 3 d. Inflowing rivers carried less leachable particulate P ($\bar{x}$ = 52%, range 32–68%; Peters 1981). Consequently, nonbiological particulates will most influence the estimated size structure at the most eutrophic site in this study (Input) because that site lies closest to the major river inflows. Particulate P content may be a suitable approximation of biomass but this equivalence must eventually be examined more thoroughly.

In short, the aim of this study is to use serial filtration followed by P analysis to examine the applicability of Sheldon's hypothesis to the plankton of lakes and to determine if season or trophic state has some influence on this application.

Methods

Samples of epilimnetic water were collected with a 5 m × 5 cm Tygon tube from four stations along the trophic gradient of Lake Memphremagog, Québec–Vermont (45°N, 72°W). These sites — Input, Indian Point, Border, and Central — were used in a previous study of the P dynamics and fractions of the lake (Peters 1979) and were selected to represent most of the range in P concentration within this lake. Samples were collected approximately weekly from late May to early September 1977 and then approximately bimonthly until early May 1978.

In the laboratory, two 50-mL samples of lake water were set aside for total P analysis and 250 mL of lake water was

filtered through a prewashed 47-mm 0.45-μm millipore filter; two 50-mL subsamples of this filtrate were also set aside for determination of soluble P. Two litres of each sample was passed through a sequence of Nitex screens of porosity 102, 75, 55, 35, 20, and 10 μm. After passing each screen, two 50-mL aliquots of filtrate were removed for P analysis and the remainder passed through the next smallest sieve. To minimize the possibility of cell breakage, each screen was mounted on a Plexiglas cylinder and gentle reverse filtration (Dodson and Thomas 1964) was used in each fractionation. This usually reduced the pressure gradient across the screen to less than 1 cm of water (~100 Pa) and only reached a maximum of 10 cm when the 10-μm screen was used.

The phosphorus content of each aliquot was measured after digestion, under pressure with 0.4 g potassium persulfate (Menzel and Corwin 1965) using the ascorbic acid modification of the molybdenum blue procedure (Strickland and Parsons 1968). Particulate phosphorus in each fraction was then calculated by subtracting the estimate of soluble P from the estimate of total P in each fraction.

The observations in these analyses are the amounts of particulate P that passes a series of screens for each combination of site and date. Because these data were collected by serial filtration, any P which appears in the filtrate of a small porosity screen also appears in the filtrate of all larger screens. Consequently, the amount of P in each fraction increases with sieve size. Under Sheldon's hypothesis a constant amount of biomass should be added with each increase of one logarithmic unit in organism size. Thus these data would confirm the hypothesis, if a linear relationship exists between the particulate P in each fraction and the logarithm of mesh size. To determine this, I regressed the particulate phosphorus (PP) in each fraction against the geometric mean of each size class ($\log F$):

$$(1) \quad PP = a + b \log F$$

and as a polynomial:

$$(2) \quad PP = a + b \log F + c (\log F)^2$$

where a, b, and c are fitted constants.

If Sheldon's hypothesis holds, the log-linear model (equation 1) should fit the data and the polynomial should not significantly improve (F test) this fit.

Unfortunately, this is not a very robust test. For each date and site, the estimates of PP in different fractions are interdependent; this violates a basic assumption in regression. This interaction increases the likelihood of finding a positive relationship in the data and the small number (six) of points in each regression would make the identification of small departures from linearity difficult. On the other hand, because of this interdependence, high or low biomass in one fraction will affect estimates in all larger fractions. This increases the chance of finding nonlinearities in these data.

In the event, the log-linear relationship was usually successful in describing these data (see results). This allowed a second approach to testing the hypothesis by scrutinizing the average residuals around all regressions for consistent departures from expected. I used a nonparametric sign test to determine if any fraction was consistently above or below the regression through the points, and the means of these departures were calculated to give a more quantitative estimate of the model's shortcomings. According to the model, no fraction should consistently depart from the log-linear relationship.

Finally, the slope and the intercept of each regression were used to examine the effect of lake trophic state (as indicated by total P concentration) and the effect of season on community size structure.

TABLE 1. The effectiveness of the log-linear and polynomial models in describing the relationship between the particulate phosphorus concentrations in each size fraction and the geometric mean of the mesh sizes used to define that fraction. TP is mean total phosphorus concentrations (±95% confidence limits) in μg/L, n is the number of samples, A the number of times in which the log-linear model showed a significant relation, B the number of times in which the polynomial led to an improvement ($P < 5\%$; F-test) in the fit. The mean, median, and range of the coefficient of determinism (r^2) are also given as an indication of fit to the log-linear model.

					Coefficient of determinism		
	TP	n	A	B	Mean	Median	Range
All dates							
Input	48±5.0	16	14	5	0.82	0.92	0.19–0.99
Indian Point	20±2.8	17	13	6	0.74	0.83	0.00–0.94
Border	15±1.6	17	15	3	0.72	0.86	0.06–0.93
Central	13±1.8	19	12	1	0.63	0.58	0.00–0.99
All		69	55	15	0.74	0.86	0.00–0.99
Summer							
Input	46±8.0	13	13	5	0.93	0.93	0.87–0.99
Indian Point	19±2.4	14	13	6	0.84	0.85	0.59–0.96
Border	15±1.6	14	14	3	0.82	0.87	0.42–0.93
Central	12±1.2	14	10	1	0.70	0.82	0.00–0.99
All		55	50	15	0.82	0.87	0.00–0.99

Results and Discussion

The log-linear model was largely successful in describing these data and so this analysis offers support to Sheldon's hypothesis. Table 1 shows that, overall, 78% of the 69 regressions showed a significant positive relationship between particulate P and the logarithm of filter size. However, in 25% of these cases (and 20% of all cases), the polynomial regression significantly improved the fit. Consequently, although Sheldon's model may be a useful tool, it is not perfect; exceptions occur in a significant number of cases. This should be expected as the size distributions presented in the paper by Sheldon et al. (1972) also show significant departures in some samples and the model is described only as a "first approximation." At least as a statement of general trend, the model is confirmed by Table 1.

Table 1 uses the coefficient of determinism (r^2) as an index of fit. Because the interdependence of the different P fractions tends to inflate indices of fit, the usual statistics are misleading. In particular, r^2 does not represent the proportion of the variance among size classes that can be attributed to size. The statistic does provide a familiar measure of scatter about the regressions. As r^2 is not normally distributed, Table 1 lists

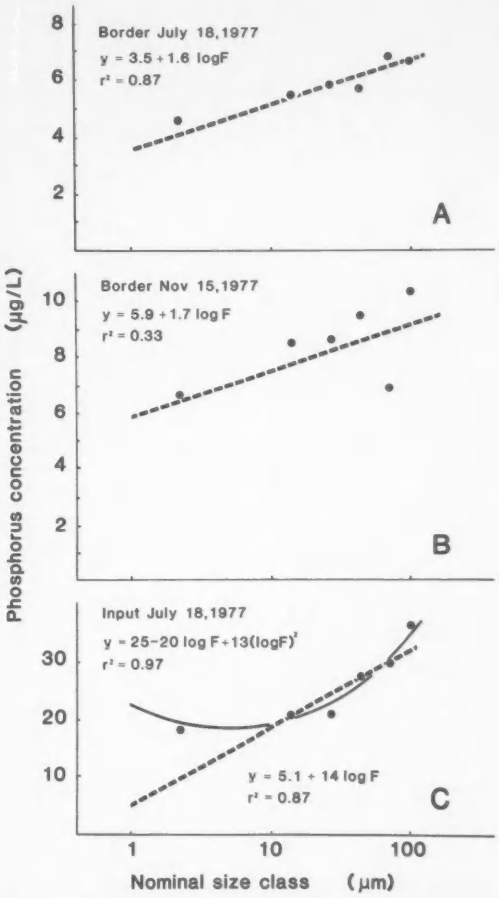

FIG. 1. Three representative curves relating particulate phosphorus concentration to the logarithm of mean organism size. (A), representative fit for all summer regressions as indicated by the median value of r^2. (B), the median fit of all nonsignificant regressions. (C), representative case in which a polynomial fit produced a significant improvement over the log-linear equation. This case showed the median increase in r^2.

both median and range of r^2 as well as the mean. To give further reality to these values, Fig. 1 shows the median case for all summer regressions (June–October), the median case for all nonsignificant regressions, and the median improvement (i.e. the case of median increase in r^2) offered by the polynomial.

An analytical problem in these data is illustrated by Fig. 1. Occasionally, the P concentration in one fraction was greater than that in the next largest. This must represent an analytical error and obviously contributes both to the nonsignificance in Fig. 1B and to the improvement offered by the polynomial in Fig. 1C. In 14 cases, at least one value exceeded the next largest fraction by more than 10% of the total P concentration. This did not appear to be a major contributor to the polynomial, for only 1 of the 15 cases in which a polynomial improved the fit showed so large a source of error. However, this was the case in 11 of the 15 nonsignificant relations. Analytical errors may therefore contribute much to some (not to all) of the apparent failures of the hypothesis in Table 1.

TABLE 2. Results of the sign test for the significance of any tendency for the P content of any fraction to lie off the regression line of particulate P on log filter size in a significant number of cases. ns, no tendency; +, the fraction contains more P than expected in a significant number of cases; −, the fraction contains less than expected. Only data collected from June through October were used in these comparisons. (*$P < 0.05$, **$P < 0.01$.)

	Fraction, µm					
	0.45–10	10–20	20–35	35–55	55–75	75–102
Input	ns	ns	ns	ns	−*	ns
Indian Point	ns	−*	ns	−*	−*	ns
Border	+*	ns	ns	−*	−*	+**
Central	ns	ns	ns	ns	ns	ns
All	+*	ns	ns	−*	−*	+*

The likelihood of erratic values increased in more nutrient-poor sites and in winter. At oligotrophic sites, a small absolute error is likely to have a large proportionate effect on the estimate of P concentration in each fraction whereas this same error would have little effect on regression for richer sites. This must contribute to the higher values of r^2 in the richest site. In winter, total biomass in all fractions was often reduced so again the possibility of small errors affecting the regressions was higher.

As Table 1 shows, 91% of the regressions for data collected from June 7 through October 8, 1977, were significant. Of the 14 remaining ("winter") regressions, 10 were not significant. In addition, the mean r^2 values increase by an average of 0.09 when winter values are removed from the calculation. Thus, if the winter values are ignored either because they are more subject to error or because winter biomass relations do not fit Sheldon's model, then the remaining data give stronger support to the applicability of that hypothesis to lake systems, at least during the main period of biological activity.

The applicability of Sheldon's hypothesis was further tested by examining trends in the residual variation. Two approaches were taken. First a nonparametric sign test was applied to determine if any size class consistently departed from the model. The sign test was used to minimize the effect of occasional analytical error and to avoid the possible effect of occasional dominance by a single class which might inflate the mean departure. The sign test also permits the pooling of all data to increase statistical power. In addition, the mean residual and the 95% confidence limits around each mean were calculated for each fraction.

Table 2 shows that when the different sites are considered independently, the fractions between 35 and 75 µm consistently contained less P than would be expected. Pooled data from all sites confirmed this and also indicated that biomass in the smallest (0.45–10 µm) and largest (75–102 µm) fractions was frequently greater than expected.

Parametric analyses (Table 3) give further support to these

TABLE 3. The mean residual (±95% confidence limits) associated with each fraction at each site (in μg P/L). Only summer values are used.

	Fraction					
	0.45–10	10–20	20–40	40–55	55–75	75–102
Input	1.10±0.1	0.37±0.44	−0.80±0.82	−0.42±0.88	−0.85±0.50	1.10±0.60
Indian Point	0.83±0.44	−0.44±0.34	−0.02±0.44	−0.56±0.46	−0.50±0.36	0.55±0.36
Border	0.23±0.25	0.01±0.46	0.09±0.46	−0.40±0.22	−0.45±0.22	0.44±0.07
Central	−0.12±0.28	0.12±0.36	−0.10±0.24	−0.24±0.20	−0.22±0.28	0.34±0.20

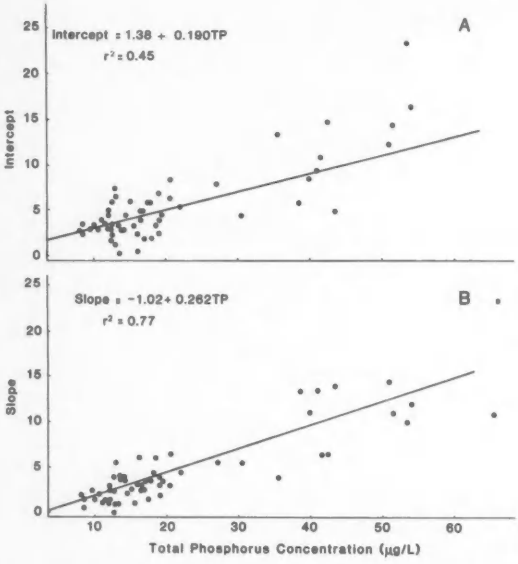

FIG. 2. Effect of total P concentration on (A) the intercept and (B) the slope of log-linear regressions between particulate P in each fraction and organism size. Only summer data (June–Oct.) were used to construct these figures.

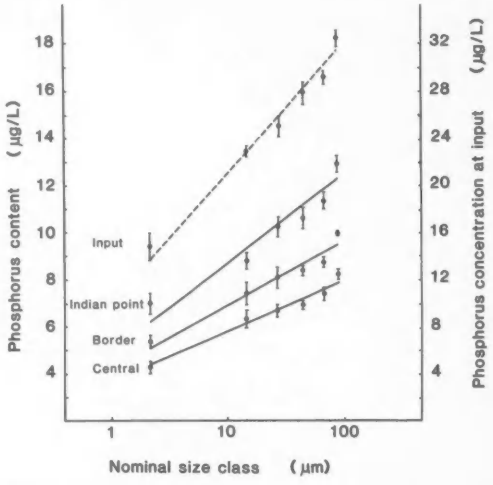

FIG. 3. Average curves for each of four sites constructed using the equations in Fig. 2 and the total P values in Table 1. Points indicate typical departures from expected, and vertical lines the 95% confidence limits on these departures (Table 2).

patterns and quantifies the average departures from the model. Neither Table 2 nor Table 3 gives support to the hypothesis that trophic state influences the application of Sheldon's hypothesis.

Departures from the model can be compared with average descriptions of the distribution of P among different size classes. Such average descriptions were generated by regressing the intercepts and slopes of all summer regressions relating P concentrations to log F against total P concentration (Fig. 2). Both regressions were significant at the 0.01% level.

Mean summer values for total P at each site were substituted into the equations in Fig. 2 to yield average intercepts and slopes for each site. These were used to plot the smooth curves in Fig. 3. The average residuals in Table 3 were then added to, or subtracted from, the value expected on the basis of these curves and the 95% confidence limits added. Figure 3 shows that the departures from the log-linear model are relatively small. However, the confidence limits are often as large as the increment from one size class to another, especially among the closely spaced classes with small biomasses between 35 and 75 μm. In other words, some incremental fractions may, at times, contain no biomass. Again, although Sheldon's model may provide an approximate description of the size structure of pelagic communities, it is not without flaws.

Sheldon et al. (1972) extended their relationship from the plankton to propose that "roughly equal concentrations of biomass occur at all particle sizes within the range from 1 to 10^6 μ, i.e. from bacteria to whales." Sufficient information is available to extend the present analyses to zooplankton and fish in Lake Memphremagog (Table 4). From the volume of the trophogenic zones of the basins in Lake Memphremagog and their P concentrations, a biased average P concentration for the lake (14 μg/L) may be calculated. This may be applied to the equations in Fig. 2 to yield estimates of the amount of material in size classes: <1 μm, 1–10 μm, and 10–100 μm. If one permits the assumption that zooplankton biomass approximates the biomass in the size class between 100 and

TABLE 4. Amount of phosphorus in $\log_{10}$ size classes in Lake Memphremagog. Approximate 95% confidence limits were generated for the planktonic classes by calculating the upper and lower 95% limits for the slope and intercept (Fig. 4) and using these values to determine probable upper and lower concentrations in each size class. P contents and confidence limits for the larger size classes are taken from Nakashima and Leggett (1980).

Group	Size range (μm)	P (μg/L)
Plankton	0.1−1	2.7±0.8
Nannoplankton	1−10	2.7±0.8
Netplankton	10−100	2.7±0.8
Zooplankton	100−1000	3.0±0.9
Fish[a]	10^4−10^6	7.0±1.4

[a]This group represents two size classes.

1000 μm and that fish biomass approximates that in the two classes in the range 1−100 cm, then the applicability of the model can be tested over the entire size range of limnetic organisms.

Nakashima and Leggett (1980) estimated the P content of zooplankton and fish in the south basin of Lake Memphremagog. As standing stocks of most organisms in the basin are twice the stocks of those elsewhere in the lake (Dermott et al. 1977; Gascon and Leggett 1977; Nakashima and Leggett 1975; Ross and Kalff 1975; R. Schoenert, Biology, McGill University, unpublished data), biased averages for the biomasses of zooplankton and fish in the lake can also be calculated.

The size class from 1 to 10 mm is not shown in Table 4. This class may represent elements of larger zooplankton, larval fish, aquatic insects, the littoral epiphytic fauna, or the benthos. We lack estimates of these classes which would allow them to be included in this analysis. The information that is available shows that the amount of material in logarithmic size classes is, to an order of magnitude, constant.

Figure 2 shows that the intercepts and slopes of these regressions increase with lake trophic state. The higher intercept indicates only that the biomass in the smallest size class increases with lake P level and the higher slope shows that larger fractions also contain more material at more eutrophic sites. This is scarcely surprising. Season appears to have some effect on the applicability of the model, for more nonsignificant regressions were found in winter. This seasonal effect is also shown if summer and winter estimates of slopes and intercepts are compared. At all sites, the mean value of the intercept rose in winter and that of the slope fell. On average, the former increased to 148% whereas the latter decreased to 54% of the estimates for June−October. This suggests that the winter community is dominated by smaller organisms. Finally, multiple regression of summer slopes and intercepts on both total P (μg/L) and Julian day (D) showed that date had a significant ($P < 5\%$; F-test) positive effect on the intercept but no significant effect on slope. The multiple regression equation for this analysis is intercept $= -3.5 + 0.17\ \mathrm{TP} + 0.025\ D$ ($R^2 = 0.55$). The effect of date was too weak to provide much more predictive power but the result does suggest some tendency for the amount of particulate P in the smallest fraction to increase with seasonal succession.

The relations in Fig. 2 offer the possibility of approximating the size distribution of the plankton in other lakes. To examine this, single samples were taken in other lakes during the summer of 1979. Unfortunately, the Nitex screening used that summer was heavily impregnated with some material which analyzed as phosphate and, despite repeated washings, contamination was obvious in all oligotrophic lakes. Samples from three eutrophic sites in Ontario (Grenadier Pond: 43°38′N, 79°28′W; Heart Lake: 43°45′N, 79°47′W; and Georgian Bay at Wasaga Beach: 44°31′N, 80°01′W) contained so much P that the effects of this contamination were minimized. Data relating P content and size from these three sites plus similar data (Peters 1978; Peters unpublished data) from August 1972 in Lakes 227 and 304 of the Experimental Lakes Area of northwestern Ontario were then regressed to yield estimates of the slope and intercept for five additional lakes.

The predictive power of the relationships in Fig. 2 for individual samples is reduced because of the broad confidence limits around individual estimates. Some power is achieved because 7 of the 10 estimates of slope or intercept fall within the confidence bands or their extrapolation (Fig. 4). The equations in Fig. 2 were incapable of predicting the size structure of the plankton of the two most eutrophic lakes (Lake 227, Grenadier Pond) but these lakes lie outside the range of observations used to build the predictions, so those comparisons may be inappropriate. In any case, the low slopes in both lakes show that larger size classes play smaller roles than would be expected from Lake Memphremagog and the high intercept in Lake 227 shows dominance by the smallest size class. Figure 4 offers only circumstantial support at best that the size structure of the plankton may be predicted from trophic state. Nevertheless the approach should be pursued further because it permits an interaction between current models which predict the P concentration of lakes (Dillon and Rigler 1975; Vollenweider 1975) and, through community size structure, the allometric literature. These two areas are among the most powerful sources of contemporary ecological prediction.

Finally, the implications of Sheldon's hypothesis for community structure and dynamics should be considered. If biomass is constant over all size classes, planktonic grazers should be able to make equally effective use of all size classes. However, because residual analysis shows that the fractions between 35 and 75 μm are frequently reduced, only grazing on nannoplankton (<35 μm) offers a continual food supply.

Under Sheldon's hypothesis the biomass (B_i) in each fraction (i) should be a constant (k):

$$B_i = k. \quad (3)$$

If W_i is the nominal size in each class, the number of particles in each class (N_i) should decline as:

$$N_i = B_i/W_i = kW_i^{-1}. \quad (4)$$

A continuous equation describing the number of organisms at each size can be calculated as the first differential of

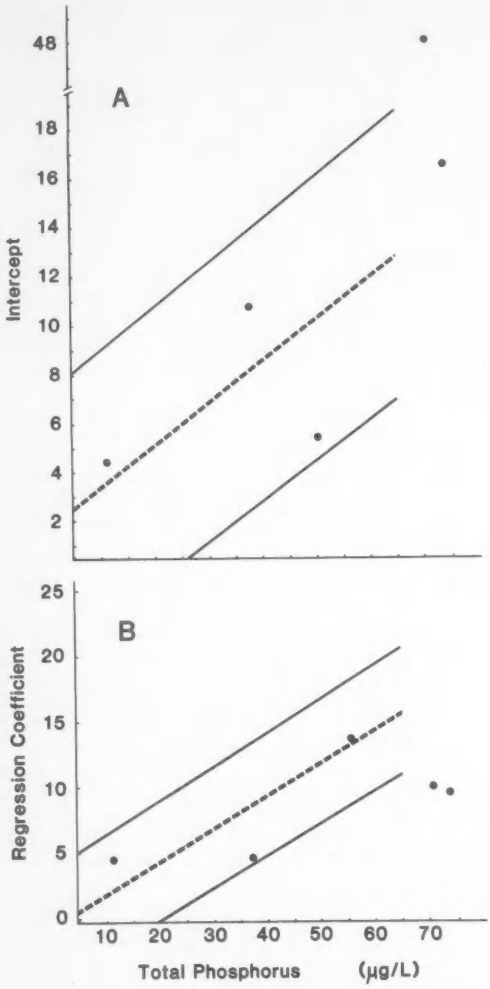

FIG. 4. An evaluation of the predictive power of the relations in Fig. 2 by comparing the confidence limits on individual predictions from these relations with the observed values in five other lakes. The statistics required to calculate these confidence limits are for slopes $Sxy = 2.17$, $\bar{x} = 28.4$, $n = 55$, $\Sigma x^2 = 13010$; and for intercepts $Sxy = 3.17$, $\bar{x} = 28.4$, $n = 55$, $\Sigma x^2 = 13010$.

equation 4 with respect to size:

$$(5) \quad dN_i/dW = kW^{-2},$$

where W replaces W_i to indicate that a continuous variable is considered. The rate of any dynamic process (R) performed by these organisms can then be described as the product of kW^{-2} and the allometric equation ($Y = aW^b$) relating rate to

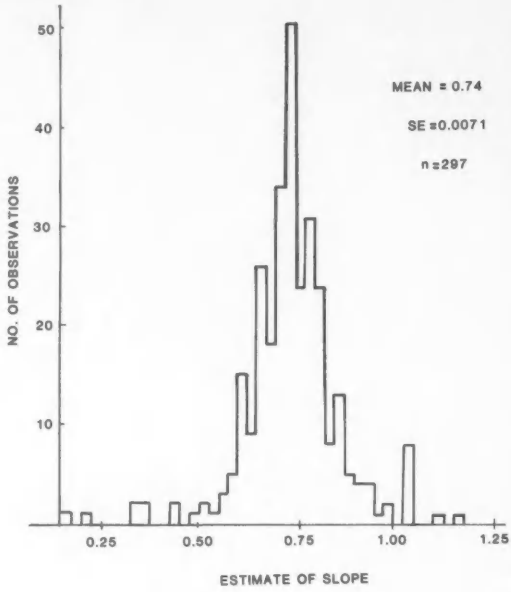

FIG. 5. Frequency distribution of the slope in interspecific allometric relations relating biological rates to individual size (data from Peters 1983).

individual size:

$$(6) \quad R = aW^b\, kW^{-2} = k'W^{b-2}.$$

A recent review of the literature concerning interspecific allometric relations (Peters 1983) lists almost 300 estimates of b in equations describing as many biological rates for as many organismic groups as could be found. The mean of the distribution (Fig. 5) is not significantly different from Kleiber's (1961) widely cited value of 0.75. Substituting this for b in equation 6, then integrating over size yields:

$$(7) \quad R_i = k'W_i^{-0.25}.$$

The contribution of different size classes to any community dynamic declines with size. Small organisms should dominate most limnetic processes.

This study lends substantial support to Sheldon's hypothesis that pelagial biomass is approximately evenly distributed among logarithmic size classes and extends this to summer limnetic communities. Much more work is still required to test the applicability of the hypothesis in other lakes, to remove ambiguities associated with fractionation by screening or the use of particulate phosphorus as an estimator of biomass, to examine the existence and generality of consistent departures from the model, and to explore the implications of model and departures for community process. Both

the model and my data suggest that tiny organisms dominate the community numerically and metabolically. If these patterns prove consistent, Sheldon's approach may permit the fusion of theories predicting lake trophy and those describing allometric behavior to yield a corpus of predictive theories with implications at both the ecosystem and community levels.

Acknowledgments

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A Revised Classification of Lakes Based on Mixing[1]

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LEWIS, W. M., JR. 1983. A revised classification of lakes based on mixing. Can. J. Fish. Aquat. Sci. 40: 1779–1787.

Deficiencies in the Hutchinson–Löffler classification of lakes based on mixing are reviewed and organized under the following headings: (1) exclusion of shallow lakes, (2) unsatisfactory relationship between meromixis and the six basic lake types, (3) excessively complex treatment of tropical lakes, and (4) difficulties in classification of cold lakes due to the 4°C boundary on cold monomixis. A revision remedies these deficiencies with minimal changes in terminology and conceptual foundation of the original classification. The revision incorporates the following features: (1) the meromixis/holomixis dichotomy is combined with the six lake types based on seasonal mixing in such a way that the two systems are hierarchical and universal; meromictic lakes are assigned to a seasonal type on the basis of the behavior of the upper water column, (2) oligomixis is eliminated, (3) shallow lakes are brought under the classification by definition of four polymictic types based on ice cover and frequency of mixing. Dependence of the eight mixing types of the revised classification on latitude, elevation, and depth is estimated from existing data, and examples are given of each type.

LEWIS, W. M., JR. 1983. A revised classification of lakes based on mixing. Can. J. Fish. Aquat. Sci. 40: 1779–1787.

L'article qui suit contient une analyse des lacunes dont souffre la classification de Hutchinson–Löffler des lacs, fondée sur le mélange. Ces lacunes ont été organisées comme suit : (1) exclusion des lacs peu profonds, (2) relation inadéquate entre la méromixie et les six types de lacs fondamentaux, (3) traitement excessivement compliqué des lacs tropicaux et (4) difficultés à classifier les lacs froids à cause de la limite imposée par la température de 4°C à la monomixie froide. Je propose de remédier à ces lacunes par des changements minimes de terminologie et de fondement conceptuel à la classification originelle. Ma révision introduit les caractéristiques suivantes : (1) la dichotomie méromixie/holomixie est combinée avec les six types de lacs fondés sur le mélange saisonnier de façon que les deux systèmes soient hiérarchiques et universels; les lacs méromictiques sont placés dans un type saisonnier en se fondant sur le comportement de la partie supérieure de la colonne d'eau, (2) l'oligomixie est éliminée, (3) les lacs peu profonds sont introduits dans la classification en définissant quatre types polymictiques reposant sur la couverture de glace et la fréquence du mélange. Des données existantes servent à illustrer la façon dont les huit types de mélanges de la classification révisée dépendent de la latitude, de l'altitude et de la profondeur, avec exemples de chaque type.

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MANY lake classification schemes have been proposed, but only the trophic classification of Naumann (1919; Hutchinson 1973) and the mixing classification of Hutchinson and Löffler (1956) are today in common use. These two classifications have probably persisted because of their simplicity, and because they are based on two of the most fundamental means for comparing lakes — nutrition and temporal variation. Classification schemes are never wholly satisfactory, but the trophic classification seems to have found broad

acceptance. The Hutchinson–Löffler mixing classification is also both reasonable and useful, as shown by its inclusion in most limnology textbooks (Ruttner 1963; Dussart 1966; Bayly and Williams 1973; Wetzel 1975; Maitland 1978; Cole 1979). Despite its wide appeal, however, the mixing classification continues to be the target of ad hoc revision, suggesting that it might be improved by some comprehensive changes.

As explained by Hutchinson and Löffler (1956), their mixing classification is successor to Forel's (1895) even simpler classification (and its modification by Yoshimura 1936), which was nomenclaturally misleading and did not adequately separate the major lake types. The Hutchinson–Löffler classification is much better in these respects but should be revised for several reasons, especially to make it conform better to extensive thermal data taken outside the middle temperate latitudes over the last 25 yr. Numerous attempts, many of which will be cited below, have been made to change the Hutchinson–Löffler classification. These have been mostly unsuccessful. Attempts at revision may have failed because they were either too drastic or because they focused too specifically on one particular point. The revisions I suggest attempt to deal comprehensively with the problems raised by the classification. At the same time, terminology and conceptual boundaries between lake types are kept as near to the traditional as possible. To a large extent my revision is merely an integration of many separate suggestions made by those who have used the classification and noted some deficiency in it.

The Present Classification System and Its Deficiencies

The Hutchinson–Löffler classification recognizes six lake types as follows:

1) Amictic: always ice-covered;
2) Cold monomictic: ice-covered most of the year and warming sufficiently to thaw but not to exceed 4°C;
3) Dimictic: ice-covered part of the year, stably stratified part of year, and mixing in spring and fall;
4) Warm monomictic: never ice-covered, mixing once per year, and stably stratified the rest of the year;
5) Oligomictic: never ice-covered, stratified most of the time but cooling enough to mix at irregular intervals longer than 1 yr;
6) Polymictic: never ice-covered, stratified, but with several episodes of complete mixing per year.

These types are only for "lakes deep enough to stratify," i.e. shallow lakes are not included in the typology. Hutchinson and Löffler predicted the approximate distributions of the six lake types, and Hutchinson (1957) elaborated on the distributions and on the variations of each type.

The amictic type is rare, as it is limited to the highest latitudes and the highest elevations outside the polar regions. Walker and Likens (1975) have pointed out that the nomenclature might suggest that amictic lakes are completely stagnant, which is not the case. For classification purposes, however, "mixing" as used by Hutchinson and Löffler refers specifically to homogenization of the entire water column. Deep turbulence or thickening of the mixed layer are not sufficient.

Hutchinson and Löffler also pointed out that the cold monomictic type is rare, as it occurs only at extreme latitudes or high elevations. The temperate zone is dominated by dimictic and warm monomictic lakes, which together outnumber all other types in the classification.

The Hutchinson–Löffler typology is most speculative in its treatment of tropical lakes. Hutchinson and Löffler predicted that in the Tropics polymixis would be dominant at high elevations, warm monomixis would be dominant at middle elevations, and oligomixis would be dominant at low elevations. They reasoned that all elevations would share a muted seasonality, but that the base temperatures would differ according to elevation. As the rate of density change increases with the base temperature, the muted seasonality of the Tropics would, they believed, result in persistent stratification at low elevations and emphemeral stratification at high elevations. Thus polymictic lakes would be found at high elevations, oligomictic lakes at low elevations, and warm monomictic lakes between these. These conclusions were reached, however, before the availability of extended thermal records for tropical lakes. Complications appeared even in the original publication, which gave Lake Victoria and several other lakes at low to moderate elevations in the Tropics as examples of the polymictic type, in apparent contradiction to the predicted restriction of this type to higher elevations. Hutchinson (1957) also indicated that lakes with daily mixing are to be called polymictic if they are tropical, although shallow temperate lakes that might mix daily were clearly excluded from the original version of classification.

The concept of meromixis, although usually treated separately, is closely related to the Hutchinson–Löffler classification. Hutchinson (1957), following Findenegg (1935), defined a meromictic lake as "a lake in which some water remains partly or wholly unmixed with the main water mass at the circulation periods." A lake that is not meromictic is holomictic. A holomictic lake belongs to one of the six mixing types, unless it is shallow.

Löffler (1957, 1958, 1964, 1968) was first to begin modifying the Hutchinson–Löffler classification. He split the polymictic category into two types, warm and cold polymictic, both of which are tropical. The basis of separation is an arbitrary boundary on maximum temperature (10°C) for lakes that do not stratify stably. Löffler (1968) defended the exclusion of shallow lakes from the classification, since he believed that inclusion of these lakes would make the classification too complex.

Paschalski (1964) suggested subtypes for the Hutchinson–Löffler classification and showed that there is historical precedent for an alternate system, which he called "European" (the origins of both Hutchinson and Löffler notwithstanding). The "European" system has not been widely accepted, probably because it is somewhat more complex, and, as pointed out by Paschalski, is more parochial to the temperate zone. Other suggested revisions of more limited scope are very numerous. Dussart (1966) used the Hutchinson–Löffler classification but modified the distribution diagram in order to show that polymictic lakes could occur outside the Tropics, as suggested

by Paschalski (1964). Walker and Likens (1975) broadened the polymictic category in a similar way, as have a number of others who have studied shallow lakes (e.g. Harvey and Coombs 1971).

In surveying the lakes of Australia, New Zealand, and Tasmania, Bayly and Williams (1973) found it necessary to introduce a new lake type in order to have an appropriate niche for lakes that develop ice cover in the winter, and rise well above 4°C in the summer, but fail to stratify stably. Berg (1963) noted similar inadequacies in coverage of North American lakes that warm above 4°C but do not stratify. Cole (1979) pointed out that some deep lakes of the temperate zone (Ohrid, Tahoe, Maggiore) must logically be called oligomictic, as they mix completely only at intervals of several years. Walker and Likens (1975) suggested complete elimination of the oligomictic category because of its ambiguity: the distinction between oligomictic and meromictic lakes is difficult. They also suggested that the meromictic/holomictic dichotomy be formally combined with the Hutchinson–Löffler classification.

Features of the Hutchinson–Löffler classification that have stimulated the above-mentioned changes in usage can be grouped under four headings:

1) Exclusion of shallow lakes from the classification;
2) Unsatisfactory relationship between meromixis and the six basic lake types;
3) Excessively complex treatment of tropical lakes;
4) Difficulties in the classification of cold lakes resulting from the 4°C temperature boundary on cold monomixis.

The exclusion of shallow lakes was not an oversight but is probably unnecessary and produces considerable difficulties. Shallow lakes are common or even dominant in some lake districts. Limnologically significant examples are numerous, including Lake George in Uganda, Lake Wingra in Wisconsin, Loch Leven in Scotland, Lough Neagh in Ireland, Lake Suwa in Japan, Lake Sibaya in South Africa, Lake Balaton in Hungary, and others. The minimum depth required to bring a lake under the classification is not constant; it varies as a function of lake size, latitude, elevation, and a number of other factors. Thus a small temperate lake 15 m deep may be clearly dimictic, whereas a large windswept lake of the same depth might never achieve stable stratification.

Hutchinson (1957) recognized the interaction between depth and mixing by creating a separate classification that combines the older depth classifications of Whipple and Birge (see Hutchinson 1957). According to Hutchinson's depth classification, lakes would be first, second, or third class depending on whether their bottom temperatures varied none, some, or much from the annual minimum. The basis of this classification is different enough from that of the mixing classification that the two do not blend easily. The general trend has been to ignore the depth classes.

Confusion between meromixis and Hutchinson–Löffler lake types can occur when meromixis is not maintained by a permanent density gradient. In the most distinctive cases of meromixis, the mixolimnion is separated from the monimolimnion by a chemocline, below which high concentrations of dissolved solids cause a density increase. Not all lakes that fit the definition of meromixis have this characteristic. For example, Åberg and Rodhe (1942), Hutchinson (1957), and Wetzel (1975) describe a meromictic phenomenon that occurs in small temperate lakes during years with rapid spring warming. Under such circumstances, a lake may enter stable stratification without having become completely homogeneous under the influence of the wind. In years without complete mixing, normally dimictic lakes are properly classified as meromictic. One is left with the impression that the classification is forcing an inappropriate application of terminology in such cases.

A similar situation arises in a different way when a deep or well-sheltered lake with strong warm monomictic or dimictic tendencies fails to achieve chemical homogeneity during the seasonal period of deep mixing but does mix enough to prevent dissolved solids accumulation in deep water. For example, Lake Malawi mixes deeply each year (Talling 1969). Because of its great depth the lake does not achieve chemical uniformity during the seasonal mixing, yet it lacks density stratification maintained by dissolved solids. Thus, although it shows clear affinities with the warm monomictic type, Lake Malawi must be classified as meromictic, because it does not achieve complete chemical uniformity at the time of mixing. Among lakes that freeze, Lake Baikal does not mix completely, despite pronounced mixing seasons (Hutchinson 1957). Confusion is added by the possibility that even such a deep lake may mix completely at long intervals, which would change the classification from meromictic to oligomictic. Classification of such lakes either as meromictic or oligomictic would obscure the fact that there is a regular seasonal deep mixing that is functionally of great importance.

Walker and Likens (1975) suggested that meromixis be combined with the other lake types. This seems reasonable insofar as a meromictic lake can be viewed as one extreme of a spectrum of mixing frequencies. Paschalski's (1964) "European" system in fact incorporates this concept and thus provides a precedent. This approach has some disadvantages, however. First, meromixis is not usually subject to direct climatic control, as are the seasonal mixing regimes. In fact a meromictic lake will typically show in its upper water column (mixolimnion) the characteristics of one of the Hutchinson–Löffler lake types. Climate and elevation impose a set of seasonal mixing phenomena in the upper water column, while some combination of geochemical, morphometric and biotic factors impose meromixis simultaneously. Thus it does not seem correct to consider meromixis simply as a parallel category to dimixis or warm monomixis.

For tropical lakes, some classification difficulties can be traced to an underestimation of the importance of seasonality. Although the amplitude of seasonality is comparatively low in the Tropics, definite annual cycles affecting insolation, air temperature, wind strength, humidity, and rainfall are the rule rather than the exception. That regular meteorological cycles of such low amplitude could induce annual patterns in lakes has now been amply demonstrated, especially over the last 20 yr. The broadest coverage of tropical lakes has been in Africa. In the single most important publication relevant to lake classification in the Tropics, Talling (1969) reviews thermal data for a great variety of lakes extending from the northern limit to the southern limit of the African Tropics and including a great range of elevations. Talling's review gives examples of lakes that, because of great depth or a

combination of effective sheltering and high relative depth, do not become chemically homogeneous on an annual basis (see also Wood et al. 1976). More importantly, he also shows that such lakes as well as lakes that do become chemically homogeneous annually are united by a common tendency to show deep mixing and minimal stability at a particular time of year, i.e. there is a universal tendency to warm monomixis. Furthermore, he shows that there is a strong tendency for the mixing season to coincide with the hemispheric winter, suggesting that minimum air temperature is of key importance. Lakes just on the equator may have an annual regime influenced by other aspects of weather, but nevertheless tend to mix at a particular time of year.

The strong trend for African tropical lakes to show warm monomixis has also been found outside Africa. Lake Lanao in the Philippines (Lewis 1973) and Lake Valencia in Venezuela (Lewis 1983) are both warm monomictic. Lake Valencia, which was studied for 5 consecutive years, has an annual overturn whose occurrence is predictable within an interval of 20–30 d. The thermal data of Richerson et al. (1977) on Lake Titicaca also suggest that this very high tropical lake has a predictible annual deep mixing season, as do Amatitlán and Atitlán in Guatemala (Weiss 1971a, b). Green et al. (1976) found that the small Indonesian Lake Lamongan (7°S) showed overturn in July, in accord with the general trend toward winter mixing. This is an especially significant example, as data for Lamongan and other Indonesian lakes visited by Ruttner (1931) during the warm season were apparently responsible for the importance attached to oligomixis among lowland tropical lakes in the Hutchinson–Löffler classification. Although high volume development and small size may well prevent Lamongan and other similar lakes from achieving complete homogeneity every year, deep mixing probably is a predictable annual occurrence.

Detailed studies of thermal structure in tropical lakes of moderate to large size have revealed some peculiarities about the behavior of these lakes during the stratification season. Frequent thermal profiles for Lake Lanao, Lake Valencia, and Lake Titicaca have shown that the thickness of the mixed layer varies much more between weeks in these lakes than would be expected in temperate lakes of similar size. For example, in Lake Valencia the average thickness of the mixed layer during stratification is 13 m, which is not significantly different from what one would expect for a lake of similar size in the temperate zone. However, during the stratification season, short periods of cool, windy weather can increase the thickness of the mixed layer temporarily to as much as 25 or 30 m, yet without completely disrupting stratification. When warm, calm weather returns, a secondary thermocline develops in the former mixed layer, again restricting mixing to a much thinner layer. This secondary layering may persist for a period of days or weeks, after which it is typically disrupted again by cool or windy weather.

A major increase in the thickness of the mixed layer in response to nonseasonal weather changes while the lake is stratified has been called atelomixis by Lewis (1973), who proposed that such a mechanism is very important in increasing the productivity of tropical lakes by bringing up nutrients from deep water to offset nutrient depletion during the stratification season. It is not clear whether all tropical lakes will show a tendency toward extreme variation in the thickness of the mixed layer during stratification, or whether the phenomenon is restricted to lakes of certain sizes or certain locations. Lakes of moderate to large size will be most likely to show the phenomenon simply because size is directly related to the range of variation in wind stress.

Large changes in mixing depth during stratification are identified particularly with tropical lakes because their stability is typically lower than that of temperate lakes, and possibly also because of differences in the Coriolis effect on currents in temperate and tropical lakes. Ruttner's work (1931, 1937) has often been cited in support of the notion that stability can be as high in tropical lakes as in temperate ones. However, Ruttner's comparisons were between Lunzer Untersee and various Indonesian lakes. As indicated by Ruttner in his comparisons, Lunzer Untersee has low stability due to its high elevation, which limits surface temperatures to about 19°C. As the majority of dimictic lakes become warmer than this, Lunzer Untersee understates the stability of temperate lakes. The upper limit on density difference between layers in tropical lakes is below what would be expected during stratification in most temperate lakes; the stability of tropical lakes during stratification thus tends to be less. In addition, the Coriolis effect on water currents is much smaller at low latitudes than at high latitudes. For this reason, winds over tropical lakes may be more effective agents of mixing (Lewis 1973). Lower stability and smaller Coriolis effect probably account for the sensitivity of the mixed layer thickness of tropical lakes to changes in wind strength.

Although atelomixis is a very important phenomenon biologically, it does not change the fundamental classification of a deep warm monomictic lake because it does not result in complete disruption of thermal stratification. However, it is obvious that the same phenomenon could produce complete mixing at irregular intervals in tropical lakes having depths between 10 and 50 m. This will be considered further in connection with the revised classification incorporating shallow lakes.

Lakes that are frozen most of the year and thaw during the summer present special problems because the Hutchinson–Löffler classification specifies a 4°C boundary for cold monomictic lakes. It is not unusual for perennially cold lakes to rise well above 4°C even though they do not stratify. If so they are not cold monomictic, although they obviously have great affinities with cold monomictic lakes.

A Revised Classification

A better combination should be made of meromixis and the holomictic lake types. This can be accomplished most simply, and without any major rearrangement of concepts or terminology, by making the two classifications hierarchical and universal: any lake can first be classified as either meromictic or holomictic and, regardless which of these categories is correct, can also be classified according to a typology based on seasonal patterns. Thus whereas the Hutchinson–Löffler typology has applied only to holomictic lakes, its revised form can apply both to holomictic and meromictic lakes. For meromictic lakes, a mixing type can be assigned according to the behavior of the upper water column (i.e. the mixolimnion).

Integration of the meromixis/holomixis dichotomy with the seasonal mixing types as suggested here solves many problems. In a given year, a lake can correctly be called meromictic if it does not become completely homogeneous chemically at the time of minimum stability. At the same time, it can be assigned to an appropriate seasonal mixing category. In classifying the lake, one is not forced to ignore the seasonal behavior of the lake if it should fail to homogenize completely. This system also does away with oligomixis, thus achieving the effect suggested by Walker and Likens (1975) based on their survey of meromixis. Lakes that have been called oligomictic will be meromictic in most years, and will have a seasonal classification corresponding to temperature and mixing behavior in the mixing portion of the water column. In certain years such lakes will be holomictic, but with the same seasonal classification.

The number of lake types is reduced by elimination of oligomixis, but must in turn be increased slightly to take in shallow lakes. Shallow lakes are first divided into two large categories: those that develop seasonal ice cover (i.e. for more than a few hours) and those that do not. The former are identified by the prefix "cold" and the latter by the prefix "warm." Although it could be argued that this choice of prefixes is not ideal, insofar as a "warm" lake may be quite cold to human touch, the convention is already firmly established by the Hutchinson–Löffler categories and is succinct if not fully explanatory. In either the warm or cold category, two possibilities are recognized: (1) the lake may achieve stratification for periods of days to weeks but not for entire seasons, or (2) the lake may mix daily, either in response to variations in wind or at night when heat is lost. Although some might argue that these two categories should not be separated, there are important functional differences in the two types. Stratification lasting days to weeks will span an interval significantly longer than the generation time of many plankton organisms, whereas daily stratification will not. Lakes that mix at intervals of days to weeks can be called *discontinuous polymictic* and those that mix daily or without interruption can be called *continuous polymictic*. Since there is a warm and cold type for each of these, we have a total of four possible polymictic lake types. These types include many shallow lakes, although they are not restricted merely to lakes of a certain depth. In the spirit of the original classification, the emphasis is on mixing rather than depth. Broadening of the concept of polymixis in this way to cover shallow lakes at any latitude is actually a reversion to the first use of the term in an overlooked publication by Wiszniewski (1953: Paschalski 1964).

The two types of cold polymictic lakes could be allowed to include the traditionally defined cold monomictic lakes. It seems advisable to retain the cold monomictic category as a separate type, however, to avoid confusion with traditional usage and to recognize the special properties of a lake that will, regardless of depth, show no direct stratification whenever it is ice-free. Thus any lake that does not reach 4°C will be classified here as cold monomictic. Lakes that pass from ice cover to some temperature above 4°C will be dimictic if they stratify for the whole season, discontinuous cold polymictic if they stratify for days or weeks but not the whole season, and continuous cold polymictic if they do not stratify or stratify only for hours at a time.

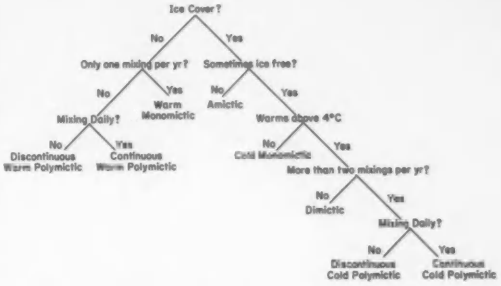

FIG. 1. The revised classification.

With the incorporation of the new types, the complete classification is as follows:

1) amictic: always ice-covered;
2) cold monomictic: ice-covered most of the year, ice-free during the warm season, but not warming above 4°C;
3) continuous cold polymictic: ice-covered part of the year, ice-free above 4°C during the warm season, and stratified at most on a daily basis during the warm season;
4) discontinuous cold polymictic: ice-covered part of the year, ice-free above 4°C and stratified during the warm season for periods of several days to weeks, but with irregular interruption by mixing;
5) dimictic: ice-covered part of the year and stably stratified part of the year with mixing at the transitions between these two states;
6) warm monomictic: no seasonal ice cover, stably stratified part of the year, and mixing once each year;
7) discontinuous warm polymictic: no seasonal ice cover, stratifying for days or weeks at a time, but mixing more than once per year;
8) continuous warm polymictic: no seasonal ice cover, stratifying at most for a few hours at a time.

Figure 1 shows the revised classification in diagrammatic form. The amictic, dimictic, warm monomictic, and cold monomictic categories are unchanged from the original classification.

In regions where deep lakes are cold monomictic, shallow lakes will be continuous or discontinuous cold polymictic. Whereas a deep lake can take up considerable heat without exceeding 4°C, a shallow lake with less water to be heated is more likely to exceed the 4° mark, which will place it with one of the two cold polymictic categories. For similar reasons, shallow lakes will often be cold polymictic in a region where deep lakes are dimictic. Thus middle to high latitudes will be rich in cold polymictic lakes wherever there are numerous shallow lakes. Much of the Arctic is in fact characterized by shallow lakes (Hobbie 1973), as are large portions of glaciated temperate areas. In view of their numerical importance, these shallow cold polymictic lakes are underrepresented in the literature. The abundance and variety of such lakes is well illustrated by the work of Harvey and Coombs (1971) on Manitoulin Island, Lake Huron. In this area deep lakes should

TABLE 1. Latitude adjustment per 100 m of elevation required to bring a lake to zero elevation for lake classification purposes.

Latitude (Degrees)	Latitude adjustment (Degrees per 100 m elev.)
0	0.27
10	0.31
20	0.34
30	0.39
40	0.46
50	0.54
60	0.68
70	0.89
80	1.3
90	2.4

be dimictic, yet of the 51 lakes they studied, Harvey and Coombs found that 41 were polymictic. Of these, two were discontinuous cold polymictic, showing stratification during calm weather, and the rest were continuous cold polymictic. Summertime temperatures are as high as 25°C in some of these lakes.

A lake that would be warm monomictic except that it is too shallow to sustain stratification for an entire season will be either discontinuous or continuous warm polymictic. A discontinuous warm polymictic lake stratifies stably for periods of days or weeks during the warm season, but cool and windy weather can mix the entire water column, temporarily disrupting stratification. A similar but even shallower lake will mix continuously or at least nightly and will thus be continuous warm polymictic.

Following the precedent of Hutchinson and Löffler (1956), it would be instructive to depict the approximate distributions of the lake types. However, expansion of the classification to include shallow lakes necessitates consideration not only of elevation and latitude, but also of depth. The three factors cannot conveniently be presented on the same graph, but elevation and latitude can be brought together under a single factor called "adjusted latitude." Adjustment of latitude merely involves adding degrees of latitude equivalent to the elevation of the lake, thus adjusting all locations to an elevation of 0 m.

Adjustment of latitude for differences in elevation is not a perfectly straightforward procedure. The effect of elevation is a function of latitude, as indicated by the different slopes of the boundary lines between lake types. The slopes of the boundary lines in the original Hutchinson–Löffler diagram were plotted against latitude, and the plot was used in defining the elevation correction for any given latitude. The corrections obtained by this method are given in Table 1. As a rough rule of thumb, for purposes of lake typology, a 200-m increment of elevation is equivalent to 1° of latitude. More exact estimates can be obtained from Table 1, but the adjustment is only approximate in any case. It is easy to see from the table that elevation is relatively unimportant to lake typology except at the highest elevations. The lake types are shown in relation to corrected latitude, depth, and fetch in Fig. 2. Of course the predicted boundaries between the categories cannot be taken too literally, as latitude, elevation, and depth are not the only factors affecting lake mixing.

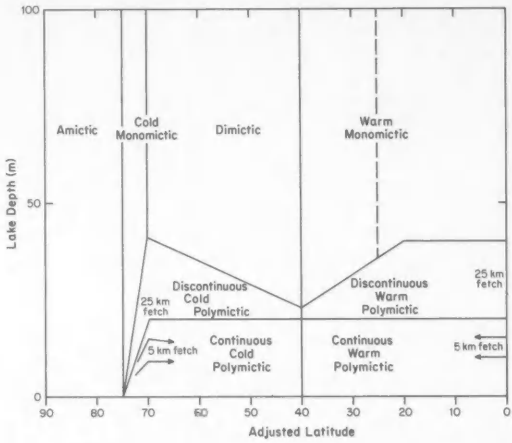

FIG. 2. Estimated distribution of the eight lake types of the revised mixing classification in relation to latitude (adjusted for elevation, see text) and water depth.

Figure 2 indicates a broader distribution for the amictic type than was originally suggested by Hutchinson and Löffler (1956). Antarctic lakes in Victoria Valley at 77°S are unequivocally amictic (Table 2). Char Lake, at 74°N, is usually cold monomictic but is sometimes amictic (Schindler et al. 1974a). The lower boundary for amictic lakes is thus set at 75°.

The upper boundary for dimictic lakes is higher in Fig. 2 than shown by Hutchinson and Löffler (1956). The valuable 6-yr study of Lake Latnjajaure by Nauwerck (1980) shows that this low-elevation lake at 68°N in Lappland is just on the border between dimictic and cold monomictic, and the detailed studies of Vorderer Finstertalersee (Pechlaner et al. 1972) show that this lake with adjusted latitude of 69° is just dimictic. The upper boundary for dimixis is thus set at 70° rather than 60° as it was by Hutchinson and Löffler. This and the lowering of the amictic boundary to 75° suggest, as indicated by present evidence, that cold monomixis occurs under a very narrow range of conditions (approximately 70–75° adjusted latitude).

Shallow lakes in the range of 70–75° may warm past 4°C and thus be either continuous or discontinuous cold polymictic. The boundaries between these and cold monomictic lakes will depend on depth and fetch. Figure 2 shows boundary lines for a fetch of 25 km. For comparison, the figure also indicates where the boundary would be for a fetch of 5 km (lines with arrows). The tendency for a shallow lake to be polymictic as opposed to monomictic obviously increases toward lower adjusted latitudes, because of greater warming. This is shown in Fig. 2 as a sloped boundary line separating monomictic from polymictic types between 75° and 70° adjusted latitude.

Deep lakes between 40° and 70° adjusted latitude will generally be dimictic, although some important variations attributable to continentality of climate are not represented in the

TABLE 2. Examples of the eight lake mixing types. Lakes marked "m" show the characteristic seasonal pattern only in the upper water column (i.e. they are always or usually meromictic).

Lake type	Name	Location, Elevation (m)	Reference
Amictic	Vanda	77S, 161E, 68	Goldman et al. (1967)
	Fryxell	77S, 163E, 22	Vincent (1981)
Cold monomictic	Char	74N, 95W, 120	Schindler et al. (1974a)
	Meretta	75N, 95W, <100	Schindler et al. (1974b)
Continuous cold polymictic	Heywood	60S, 45W, <100	Light et al. (1981)
	Smokey Hollow	46N, 82W, 190	Harvey and Coombs (1971)
	Joseph	53N, 113W, 670	Hickman (1979)
Discontinuous cold polymictic	Tobacco	46N, 82W, 228	Harvey and Coombs (1971)
Dimictic	Mendota	43N, 88W, 259	Stewart and Hasler (1972)
	Erken	59N, 18W, 11	Nauwerck (1963)
	Baikal (m)	53N, 108E, 453	Hutchinson (1957)
	Fayetteville Green (m)	43N, 76W, 278	Brunskill and Ludlam (1969)
Warm monomictic	Lanao	8N, 124E, 702	Lewis (1973)
	Windermere	54N, 3W, 39	Jenkins (1942)
	Malawi (m)	12S, 34E, 475	Talling (1969)
	Ohrid (m)	41N, 20E, 695	Hadžišče (1966)
Discontinuous warm polymictic	Rotorua	38S, 176E, 280	Cassie (1969)
	Leven	56N, 3W, 107	Bindloss et al. (1972)
	Mahinerangi	45S, 170E, 391	Mitchell and Galland (1981)
Continuous warm polymictic	George	0N, 30E, 913	Ganf and Viner (1973)
	Sonachi (m)	0N, 36E, 1889	MacIntyre and Melack (1982)

figure (Hutchinson 1957). Very shallow lakes in this range will be continuous cold polymictic. The depth boundary for this condition, as shown in Fig. 2, is determined largely by fetch. The fetch effect has been approximated according to the empirical relationship $D = 4\ F^{0.5}$, where D is mixed layer thickness (m) and F is fetch (km) (Ragotskie 1978). The figure shows the boundary for $F = 25$ km, but also indicates, by means of the short lines with arrows, where the boundaries would be for $F = 5$ km.

Below about 40° adjusted latitude, deep lakes will be warm monomictic. If they are very deep or very well sheltered, they may in addition be meromictic in most years, but this does not affect the seasonal mixing classification according to the present scheme. These lakes will show a single predictable annual period of deep mixing or complete overturn. A vertical dashed line in Fig. 2 separates the tropical from the temperate warm monomictic lakes. This dashed line is an indication that warm monomictic lakes at lower latitudes show greater fluctuations in the thickness of the mixed layer at irregular intervals during the stratification season (i.e. atelomixis). The greater irregularity of mixed layer thickness is explained by a convergence of the surface and deepwater densities and the reduced Coriolis effect along the spectrum from temperate to tropical warm monomictic lakes. This tendency will be most pronounced in lakes of moderate to large size; it will not be so noticeable in small lakes.

The shallowest lakes between 0° and 40° adjusted latitude will be continuous warm polymictic, typically losing stratification at night. Lake George, Uganda, can be considered archetypal for this category, but such lakes will also be found at high elevations in the Tropics. The type reaches its high-elevation extreme with shallow tropical lakes that are near the snowline. Such lakes may freeze at night and thaw in the daytime (Löffler 1960). Since they do not develop a seasonal ice cover, they are a peculiar sort of continuous warm polymictic lake.

As with the lakes between 40° and 70° adjusted latitude, the boundary for continuous polymixis is set by the empirical relationship between depth of thermocline and fetch. As there is presently little indication that the mean thickness of the mixed layer is significantly greater at low latitudes than at high latitudes, the same boundary is used for a given fetch as in the higher latitude ranges. However, the irregular thickening of the mixed layer at lower latitudes is more pronounced and this broadens the depth range covered by discontinuous warm polymictic lakes. The placement of the upper critical depth for the discontinuous warm polymictic category is based principally on detailed studies of Lake Lanao and Lake Valencia (Lewis 1973, 1983). Below 20° adjusted latitude, the depth range of lakes in this category is essentially constant because the difference in density between the upper and lower water column is very nearly stable between 0 and 20° latitude. From 40° to 20°, the depth range of the discontinuous warm polymictic category increases because the density difference between upper and lower water column during stratification decreases, thus increasing the likelihood that strong winds will change the mixing depth during the season of stratification.

Table 2 illustrates the application of the revised classification scheme to a diverse group of lakes. Shallow cold lakes that rise well above 4°C but mix daily when ice-free include Heywood, Smokey Hollow, and Joseph lakes. These would have been of uncertain classification by the Hutchinson–Löffler typology, but with the revised scheme they have an appropriate niche in the continuous cold polymictic category. Tobacco Lake, which is even more distant

from any of the traditional categories, shows the usefulness of the discontinuous cold polymictic category. Inclusion of Lake Baikal and Fayetteville Green Lake with the dimictic category and Lake Malawi and Lake Ohrid with the warm monomictic category shows that these lakes have pronounced seasonal cycles in addition to meromictic properties. The two warm polymictic categories appropriately separate lakes Rotorua, Leven, and Mahinerangi, which mix part of each year at odd intervals longer than one day, from lakes George and Sonachi, which mix daily.

The revised classification, like the original, separates lakes according to three criteria: ice cover, mixing, and direct stratification. As shown by Table 2, however, the revised classification not only accepts shallow lakes, but also recognizes that shallow lakes diversify the range of seasonal behavior beyond what would be expected for deep lakes only. The awkward choice between meromixis and seasonal behavior of the upper water column is avoided, but without discarding the concept of meromixis, which can be applied across the entire spectrum of seasonal mixing types. The mixing behavior of tropical lakes is recognized as simple in principle, encompassing only three basic seasonal patterns, any one of which may be superimposed on meromixis. In general the revised classification takes into account the existence at any latitude and elevation of a graded series of mixing behaviors based mainly on depth and fetch. In view of the direct connection between these gradations in mixing behavior and biological processes, the revised classification may better complement the study of lakes as dynamic ecological systems.

Acknowledgments

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Physicochemical Typologies of South-Central Ontario Lakes[1]

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ZIMMERMAN, A. P., K. M. NOBLE, M. A. GATES, AND J. E. PALOHEIMO. 1983. Physicochemical typologies of south-central Ontario lakes. Can. J. Fish. Aquat. Sci. 40: 1788–1803.

We present basic physicochemical data and principal component analyses (PCA) of both morphometric and chemical variables for 37 Ontario lakes. Multivariately derived composite variables were substituted for more conventional independent variables in several regression models. These composite variables always explained a greater percentage of variance than the standard morphometric variables. A typology derived in part from the PCA was useful in identifying groups of lakes for which the Ragotzkie model predicting maximum depth of the summer thermocline was appropriate and other groups of lakes that appear to be outliers on the basis of insufficient volume. In addition, variables important in defining the typology, particularly $\bar{z}:z_{max}$ ratio and lake volume, were shown to be among the most important in a stepwise, multiple linear regression explaining 91% of the variance in nannoplankton to filter-feeding zooplankton ratios in the lakes. This represents a 47% improvement over previously reported results. Total phosphorus still explained more variance in several measures of phytoplankton biomass than did a multivariately derived composite chemical variable, but there were significant explanatory improvements in phosphorus–phytoplankton regressions within lake groups derived from a typology based on a speciated chemical matrix. There appears to be some overlap in biological patterns from morphometrically and chemically defined lake types. We suggest that these may represent ends of a continuum of differing density regulation responses by the biological communities.

ZIMMERMAN, A. P., K. M. NOBLE, M. A. GATES, AND J. E. PALOHEIMO. 1983. Physicochemical typologies of south-central Ontario lakes. Can. J. Fish. Aquat. Sci. 40: 1788–1803.

Nous présentons les données physico-chimiques de base et les analyses en composantes principales (PCA) des variables, tant morphométriques que chimiques, de 37 lacs de l'Ontario. Les variables composites dérivées d'opérations multidimensionnelles ont remplacé, dans plusieurs modèles de régression, les variables indépendantes plus conventionnelles. Les variables composites ont toujours permis d'expliquer un plus grand pourcentage de la variance comparativement aux variables morphométriques standard. Une typologie dérivée en partie de l'analyse PCA a permis d'identifier des groupes de lacs auxquels peut s'appliquer le modèle de Ragotzkie de prédiction de la profondeur maximale de la thermocline estivale. Elle a également permis d'identifier d'autres groupes de lacs qui, sur la base d'un volume insuffisant, semblent différer des autres. En outre, on a démontré que des variables jouant un rôle important dans la définition de la typologie, en particulier le rapport $\bar{z}:z_{max}$ et le volume du lac, se classaient parmi les plus importantes dans une régression linéaire multiple par étapes expliquant 91 % de la variance dans les rapports nannoplancton : zooplancton filtreur des lacs. Ceci est une amélioration de 47 % par rapport aux résultats publiés antérieurement. Le phosphore total explique encore plus de variance dans de nombreuses mesures de phytoplancton qu'une variable chimique composite dérivée d'opérations multidimensionnelles. Il y a cependant amélioration significative des propriétés explicatives des régressions phosphore–phytoplancton parmi des groupes de lacs dérivés d'une typologie reposant sur une matrice chimique spécifique. Il semble y avoir un certain chevauchement des caractéristiques entre types de lacs définis morphométriquement et chimiquement. À notre avis, ces types peuvent représenter les extrémités d'un continuum de réactions différentes de régulation de la densité de la part des communautés biologiques.

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THIRTY-SEVEN lakes in south-central Ontario have been under study by the Lake Ecosystem Working Group (LEWG) at the University of Toronto since 1978. An important premise for LEWG was a belief that the number of ways in which lakes can differ may often preclude development of single descriptive models. From an ecosystem perspective, we felt that one of the most profitable approaches would be an initial classification of lakes into "types." Elucidation of types would then allow testing of our hypotheses concerning the roles that morphometry, the relative amounts of pelagic predation or resource limitation, stress (nutrient, fish exploitation, toxicological), and species size or mode of energy partitioning might play in determining a specific lake's type and its resultant dynamic behavior.

We used several statistical approaches to derive typological schemes based on physical, chemical, and biological parameters. Gates et al. (1983) reported on the analysis of principal component space trajectories based on year-to-year changes in the relative proportions of 16 size classes of planktonic biomass. They showed that the position of a specific trajectory's centroid was in part determined by lake morphometry whereas trajectory direction was a function of changes in annual precipitation, presumably as related to changes in chemical loading. Paloheimo and Zimmerman (1983) reported on a cluster analysis based typology for biomass in four functional categories of plankton in which within-type phosphorus–nannoplankton regression coefficients were significantly higher than the overall regression coefficient and better explained the decreasing return to scale of the phosphorus–phytoplankton relationship observed in the data set. Inclusion of morphological and chemical information did not significantly increase the within-cluster correlation coefficients. However, both morphometry and chemistry significantly increased the multiple squared R between phosphorus and nannoplankton in the data set as a whole. Both these papers began with the extant biological community and sought explanations for its structure in aspects of physicochemistry. Our study reverses the above process: it details the basic physicochemistry of the LEWG lake set, using it as the basis of multivariate typological schemes, and then looks for accompanying biological patterns.

Materials and Methods

Data Collection

The data used in these analyses are from subsets of the 37-lake LEWG set sampled between 1978 and 1981 (Fig. 1). A list of lakes, their locations, major watershed geology, and five morphometric parameters previously calculated by the Ontario Ministry of Natural Resources and/or the Ontario Ministry of the Environment, the "primary" morphometric data set ($\bar{z}$, z_{max}, AREA, VOL, PERIM), can be found as Tables 1 and 2 in Paloheimo and Zimmerman (1983). Eleven additional or "secondary" morphometric variables (Table 1), shoreline development (D_L), relative depth, $REL_{\bar{z}}$, and mean depth–maximum depth ratio, $\bar{z}:z_{max}$, were calculated for the more intensively sampled lake set (the 24 lakes in Table 1 rather than the original 37) from details in Wetzel (1975) or determined as follows. LITT, percent littoral zone, was taken as the percentage of the total sediment area to which 10% incident light penetrates. The total sediment area was calculated from the formula for the determination of the curved surface of a frustrum of a right cone using the depth contours of the bathymetric maps as the frustral altitudes. $THERM_{\bar{z}}$, maximum depth of the summer thermocline, and epilimnial thickness, $EPI_{\bar{z}}$, were taken from thermal profiles as the depth at which the second derivative of the curve of depth with respect to temperature was zero for the former and maximally positive for the latter (Ragotzkie 1978). Some examples of the variation in patterns of thermal development are presented in the first panel of Fig. 2. A_{sed}, sediment area in the epilimnion, was defined as the percentage of total sediment area above $EPI_{\bar{z}}$. V_{epi}, volume of the epilimnion, was the volume of water above $EPI_{\bar{z}}$. Ae/Ve, followed Fee (1979). LITE, epilimnetic light penetration, was defined as the difference between $THERM_{\bar{z}}$ (previously defined) and the depth of 10% light penetration for that same time period. Hence, a value less than 0 indicates a lake with at least 10% incident light at the thermocline. FETCH was taken as the longest unobstructed distance from one shore to another. Wind-weighted fetch (Smith and Sinclair 1972) was also calculated.

Temperature and light data for calculation of LITT, $THERM_{\bar{z}}$, and LITE were collected along with pH, pE, conductivity, and dissolved oxygen at 1-m intervals with a Hydrolab Surveyor or System 8000 (Hydrolab, Austin, TX) and a DPMT-100 photometer (Canadian Research Institute, Don Mills, Ont.). Lakes were sampled at approximately 2-wk intervals from mid-April through August. Each sampling circuit of the lakes is referred to as a cycle. Water samples for chemical analyses and chlorophyll were collected using a 4-m tube. Samples were collected at stations situated over the deepest part of the lake. Only results for the main basins are reported here.

Analyses were performed using standard chemical techniques (Ontario Ministry of the Environment 1981) at the laboratories of the Ontario Ministry of the Environment, Rexdale, Ont. Details of system chemistry are presented in Tables 2 and 3. The phrase "more conservative" (Table 2) is used for parameters that analysis of variance indicated did not undergo significant concentration changes ($F < 0.05$) from sampling cycle to sampling cycle. These elements were sampled on a less frequent schedule ($N = 4$), with the exception of chlorophyll ($N = 8$), and are presented without ranges. "Less conservative" (Table 3) refers to elements whose concentrations did fluctuate significantly across the summer, usually downwards from spring overturn. These were sampled every cycle ($N = 8$) and are presented along with minimum and maximum values for the element. In addition to total concentrations as measured above, the "free" phase of each element was determined from the chemical equilibrium computer program REDEQL-II (McDuff and Morel 1973). Phytoplankton and zooplankton were collected and their biomasses quantified into one of 16 ecological, size-feeding categories (Sprules and Knoechel 1983).

Data Analysis

Various combinations of morphometric and chemical parameters were entered into the Statistical Analysis System's (SAS 1981) PRINCOM procedure for principal components analysis (PCA). This analysis results in a set of uniquely

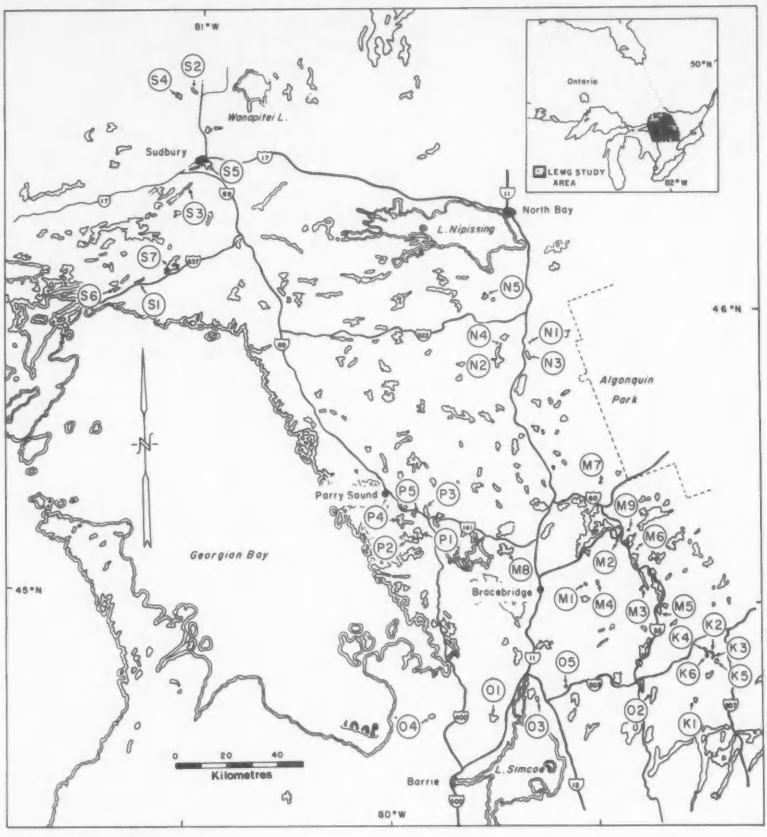

FIG. 1. The LEWG lake set.

determined, uncorrelated axes incorporating most of the variation in the data set. We chose PCA over such alternatives as cluster analysis based on the way PCA handles data reduction. While cluster analyses will always create groupings from a data set, there is a sequentially increasing loss of information. In PCA, any information loss occurs simultaneously in a well-defined manner. In addition, PCA yields unique, uncorrelated composite variables for use in additional analyses. The analyses were run on the correlation matrices due to the dimensionally inconsistent nature of the data sets. Multiple, linear stepwise regression, simple linear regression, and ANOVA (SAS) were used to evaluate the usefulness of the variables derived from the morphometric and chemical PCA axes and the value of the resultant typologies.

Results and Discussion

MORPHOMETRIC ANALYSES

Many regression-based models in limnology relate aspects of lake morphometry to some biotic parameter. Rawson (1952), Ryder (1965), Sakamoto (1966), Brylinsky and Mann (1973), Fee (1979), and Straskraba (1980) represent a few examples of post Naumann–Thienmann regression-based models. In many of these a considerable amount of variance remains unexplained and is often implicitly or explicitly attributed to the vagrancies of the dependent, i.e. biological, variable. However, as Ryder et al. (1974) pointed out, independent variables are often nonlinearly related to a host of other variables. For the specific example of the morphoedaphic index, these authors pointed out that one of the independent variables, mean depth, will also be related to percent light penetration, shoreline development, and percent littoral zone, among others, all of which will differentially affect the dependent variable.

Pursuing that example for the LEWG data set shows that mean depth correlates reasonably well with percent littoral zone ($r = -0.70$) but poorly ($r = 0.28$) with shoreline development, D_L (see Table 4). However, lakes P5 and S1 have similar mean depths (6.5 and 5.9 m, respectively) and similar shoreline development indices (4.6 and 4), while P5 has 47% of its area in the littoral zone and S1 has 85% of its area in the littoral zone. Alternatively, M2 and P2 have sim-

TABLE 1. Secondary LEWG lake set morphometry. —, lakes do not stratify.

Lake code	D_L (m)	REL_c (m)	$\bar{z}:z_{max}$	LITT (%)	$THERM_c$ (m)	EPI_c (m)	A_{sed} (km^2)	V_{epi} ($km^3 \times 10^{-3}$)	Ae/Ve ($\times 10^{-2}$)	LITE (m)	FETCH (km)
K2	2.3	2.8	0.41	30.7	6	4	0.21	4.68	4.42	0	1.82
K3	1.8	3.6	0.29	40.1	8	3	0.20	2.38	6.40	−2	1.11
K5	2.6	2.1	0.37	87.6	12	6	0.05	15.39	3.57	−1	2.30
K6	1.5	0.7	0.35	70.3	6	4	1.07	6.92	15.40	−1	1.01
M2	1.7	2.7	0.42	72.2	9	6	0.21	2.80	7.46	+2	1.48
M4	1.4	2.7	0.35	39.5	6	4	0.19	2.97	6.57	−2	1.09
M5	1.7	1.5	0.43	39.2	12	10	1.25	35.49	3.52	−3	3.91
M6	1.4	2.6	0.48	76.3	9	6	0.12	2.18	5.23	+2	0.91
M8	6.4	0.3	0.32	100.0	7	6	7.90	29.92	26.40	−3	6.87
N4	1.8	0.9	0.44	100.0	—	—	0.05	0.82	5.98	0	3.03
N5	3.0	0.9	0.39	69.5	8	6	1.23	11.28	10.09	−2	3.03
O1	1.3	0.5	0.25	97.2	—	—	2.57	13.11	19.61	+3	3.63
O2	1.9	0.6	0.44	64.3	12	8	4.05	60.71	6.67	−3	3.97
O3	1.2	0.2	0.30	100.0	—	—	0.96	1.28	75.2	0	2.06
O4	1.1	0.2	0.40	100.0	—	—	1.17	3.66	32.0	0	2.57
O5	1.1	1.0	0.41	84.5	6	4	0.47	3.16	15.1	−1	3.50
P1	4.3	2.3	0.34	35.7	9	4	1.05	39.61	2.65	−2	3.93
P2	6.3	1.3	0.28	48.7	8	6	2.14	36.81	5.81	−2	2.43
P3	4.6	0.9	0.31	47.2	8	4	1.37	17.70	7.74	−2	1.58
P4	4.8	1.8	0.24	56.9	10	6	2.26	35.47	6.37	−3	4.63
P5	3.0	1.5	0.39	55.6	8	4	0.47	7.02	6.62	−1	1.63
S1	4.0	1.1	0.40	84.5	9	6	0.78	7.57	10.30	0	3.75
S6	2.9	2.7	0.51	62.4	15	8	0.54	16.59	3.22	+3	3.11
S7	6.8	1.0	0.30	25.2	10	6	1.00	85.78	1.17	−2	6.80

ilar mean depths but quite divergent shoreline development indices (1.7 vs. 6.3) and percent littoral zones (72 vs. 48%). Such simultaneous variation among parameter relationships is undoubtedly one source of unexplained variance in simple regression models. Alternatively, such interactions may be of sufficient magnitude to preclude development of models with sufficient precision for universal applicability. Statistical methods that can deal with the structure of data set variance offer one opportunity to analyze such interrelationships and assess the implications of those relationships for model development.

We were interested in whether variables derived from PCA could provide either better predictive ability for biological parameters than standard morphometric variables or could suggest particularly useful combinations of those standard morphometric variables. We were also interested in whether lakes could be "typed" according to the values of their PCA-derived variables and whether models relating biotic and abiotic factors would have higher precision within as opposed to between lake types.

The result of one such analysis based on the primary and secondary morphometric variables for the 24 lakes listed in Table 1 is shown in Fig. 3 along with scaled outlines of the lakes. The first component (factor 1) represents a contrast between lakes with large volumes, VOL ($r = 0.85$), large maximum depths, z_{max} ($r = 0.83$), and large epilimnetic volumes, V_{epi} ($r = 0.83$), and those with large percent littoral zones, LITT ($r = -0.70$), and large epilimnetic area to epilimnetic volume ratios, Ae/Ve ($r = -0.67$). The second component (factor 2) represents a contrast between lakes with large surface areas, AREA ($r = 0.72$), and those with shallow relative depths, REL_c ($r = -0.80$), and smaller mean depth to maximum depth ratios, $\bar{z}:z_{max}$ ($r = -0.60$) (Table 5). We purposely chose to use as wide a set of different morphometric variables as possible, even if some are autocorrelated, in order to achieve the best descriptors in as unbiased a manner as possible. For example, factor 2 incorporates aspects of lake depth, yet $\bar{z}:z_{max}$ ratio and REL_c are more important in describing the variance in the lake set than z_{max} or $\bar{z}$, the more standard morphometric variables.

Two regression-based models were chosen to test our hypotheses regarding better percentages of explained variance from multivariately derived independent variables: Sakamoto's (1966) mean depth chlorophyll model ($mg \cdot m^{-3}$ $Chl = 248.3z^{-1.55}$) and Fee's (1979) productivity index for chlorophyll ($mg \cdot m^{-3}$ $Chl = 2.4 + 6.5Ae/Ve$). Prediction of chlorophyll concentration per se was not our major objective. From a production perspective, we are more interested in size classes of algal biomass than in chlorophyll concentrations (Paloheimo and Zimmerman 1983). The two models illustrated merely represent two reasonably well-known regression equations utilizing a morphometrically based independent variable. Hence, it is not the predictive power of the Sakamoto and Fee models for our data but comparisons of goodness of fit (as tests in the derivation of morphometric state variables for our lake set) that is of primary interest. Substitution of the appropriate PCA factor score for the standard morphometric variable in these models always improved the percent variance accounted for, although not necessarily by a large amount.

The fit of the LEWG data set to the original Sakamoto model is generally poor (exponents of −0.53 and −1.55, respectively), although the mean depth chlorophyll relationship is significant ($P < 0.01$). The poor fit to the original model is not unexpected given the insensitivity of a negatively sloped power function at small values of the independent

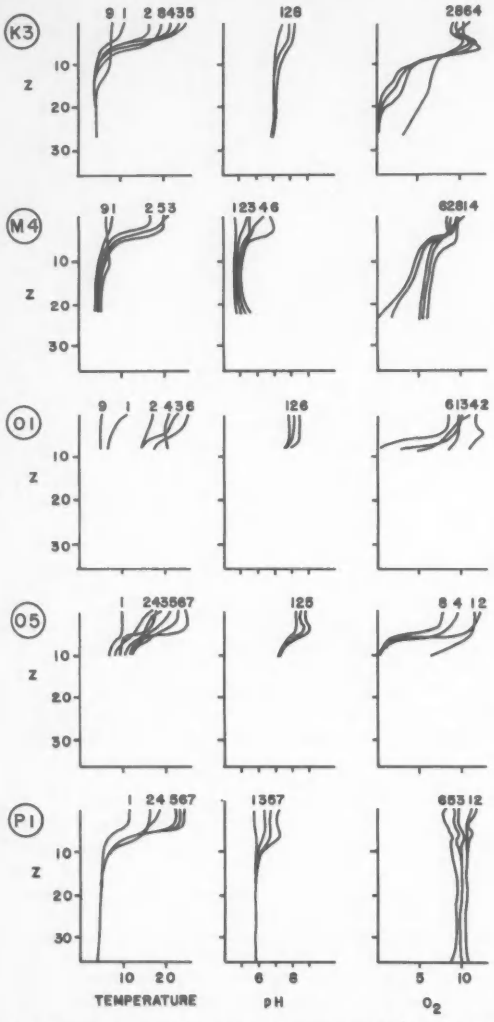

FIG. 2. Temperature (°C), pH, and oxygen ($mg \cdot L^{-1}$) profiles of selected LEWG lakes for cycles 1–9 where data do not overlap.

variable, $\bar{z}$, combined with our much narrower range of $\bar{z}$. While some of Sakamoto's values for mean depth exceeded 60 m, only eight of our lakes have mean depths greater than 10 m. Consequently, the majority occur at depths too shallow for total photosynthetic profile development and are expected to be poor approximations to the original equation (Straskraba 1980). What is of interest to us is the increase in explained variance in chlorophyll concentration when a lake's score on factor 2 (PC-2) is substituted for $\bar{z}$, as well as the increased sensitivity gained by the simplification of the relationship from a hyperbolic to a linear function.

An alternative model for prediction of chlorophyll is Fee's productivity index. Ratio Ae/Ve is correlated with $\bar{z}$ (−0.61) (Table 4) but explains a marginally higher proportion of variance (37 vs. 35%) in chlorophyll concentration. PC-2 remains the best predictor:

$$mg \cdot m^{-3}\ Chl = 0.68\bar{z}^{-0.53}, \qquad r^2 = 0.35$$

$$mg \cdot m^{-3}\ Chl = 1.5 + 6.0(Ae/Ve), \qquad r^2 = 0.37$$

$$mg \cdot m^{-3}\ Chl = 2.18 + 2.01PC\text{-}2, \qquad r^2 = 0.44.$$

Figure 3 does not provide an unambiguous morphometric typology. Lakes M8 and O3 appear to be outliers at one end of factor 2, and they do have the highest chlorophyll concentrations in the data set (7.5 and 4.8 $mg \cdot m^{-3}$, respectively); however, S7, which has the next highest factor 2 score, has a relatively low chlorophyll level (1.6 $mg \cdot m^{-3}$). Alternatively, P4 and P5 have reasonably similar chlorophyll levels (1.3 and 1.6 $mg \cdot m^{-3}$, respectively), similar mean depths (10.8 and 7.8 m), and similar Ae/Ve ratios (6.37×10^{-2} and 6.62×10^{-2}). Yet they occur in different factor space quadrants. As we discuss in the following section, these lakes exhibit different geochemistries. Algal production depends on chemical load as well as mean depth (light or grazer relationships) or Ae/Ve (nutrient or algal cell settling potential). This suggests that a PCA-derived morphometric variable may be more powerful than a standard morphometric variable only to the extent that morphometry contributes to production. In other words, a morphometrically based PCA might be expected to increase explained variance across a data set, but any additional insight within the data set (typology) will be dependent on the nature of the dependent variable.

Ragotzkie's (1978) model for prediction of the maximum depth of the summer thermocline ($THERM_z = 4\sqrt{F}$) represents a regression model in which variance should be predominately a function of morphometry. We have used this model to further explore a morphologically based typological scheme and for comparisons of percent variance explained within as opposed to across lake types.

The correlation between FETCH and $THERM_z$ in the LEWG data set is poor ($r = 0.28$) (Table 4). Correspondingly, the fit to Ragotzkie's model (Fig. 4) is not good with $4\sqrt{FETCH}$ generally underestimating $THERM_z$ for the data set as a whole. Smith and Sinclair (1972) suggested that a prevailing wind-weighted fetch is a more appropriate variable for expressing the effect of wind-driven circulation on lakes. We substituted a Smith and Sinclair wind-weighted FETCH in the analysis of $THERM_z$. However, weighting for prevailing winds effectively decreases FETCH and therefore increases the amount by which Ragotzkie's model underestimates $THERM_z$ for our lake set. Consequently, we feel neither wind-weighted nor raw FETCH alone provides an adequate description of thermal relationships across our entire lake set. Shuter et al. (1983) experienced similar problems with outliers in their analyses of thermocline relationships for both the LEWG and a continental data set.

Table 4 suggests that the best predictor for $THERM_z$ in the LEWG lake set is lake volume, even though VOL only accounts for about 55% of the variance in $THERM_z$. Given the results of substitution of composite variables in prediction of chlorophyll, it might seem that substitution of PC-1, the

TABLE 2. Mean nutrient chemistry (1980, $N = 4$) for the more conservative elements in the LEWG lake set ($mg \cdot L^{-1}$) plus chlorophyll ($N = 8$, $mg \cdot m^{-3}$). —, not sampled in 1980.

Lake code	Concentration									
	Ca	Mg	Na	K	Cl	SO_4	OC	IC	TKN	CHL*a*
K1[a]	39.00	4.90	1.10	0.95	1.40	12.00	6.70	25.80	0.44	—
K2	25.00	2.44	0.70	0.78	0.98	10.75	5.39	16.00	0.33	1.4
K3	28.25	2.83	1.18	1.21	1.90	10.00	5.79	19.00	0.33	1.5
K4[a]	26.00	3.30	1.10	1.05	1.30	12.50	5.90	17.00	0.61	—
K5	26.85	3.63	0.50	0.68	0.66	12.50	4.40	18.05	0.28	1.6
K6	26.05	2.39	2.40	0.75	0.85	0.96	11.00	5.65	16.30	2.4
M1	2.90	0.69	0.88	0.50	0.50	7.88	3.71	0.80	0.27	—
M2	2.73	0.63	0.77	0.37	0.47	7.00	2.09	0.80	0.21	0.8
M3	3.15	0.59	0.70	0.53	0.73	7.38	6.44	0.78	0.34	4.0
M4	2.30	0.55	0.68	0.41	0.46	7.88	4.68	0.25	0.31	2.7
M5	5.40	1.21	1.25	0.84	1.61	9.00	3.40	2.35	0.23	1.5
M6	2.10	0.41	0.43	0.30	0.46	6.63	2.80	0.23	0.21	1.9
M7[a]	3.20	0.80	1.00	0.60	0.60	7.50	2.10	1.00	0.26	—
M8	4.45	1.00	2.70	0.85	3.48	7.38	5.49	2.03	0.39	7.5
M9[a]	3.00	0.70	1.00	0.45	0.80	8.00	2.70	0.60	0.28	—
N1[b]	3.20	0.50	1.00	0.40	0.40	8.50	2.20	0.60	0.21	—
N2[a]	3.40	0.70	1.60	0.75	1.70	8.00	2.90	1.00	0.25	—
N3[a]	4.20	1.35	1.70	0.70	1.10	8.50	5.50	2.20	0.37	—
N4	2.40	0.54	0.73	0.51	0.38	8.38	6.23	0.38	0.34	2.3
N5	3.20	0.75	1.00	0.75	0.74	8.88	6.80	0.95	0.30	2.4
O1	41.50	9.25	2.53	1.23	2.43	13.38	4.36	33.73	0.42	4.2
O2	31.25	4.44	1.23	0.56	1.49	11.50	5.00	21.73	0.30	1.1
O3	35.50	4.31	2.40	1.10	3.45	7.88	11.16	26.00	0.69	4.9
O4	30.40	7.38	8.35	1.25	13.00	12.25	4.49	24.50	0.47	2.7
O5	27.50	5.88	4.20	0.80	8.15	12.13	5.36	19.93	0.43	2.3
P1	3.50	1.04	2.30	0.63	3.18	7.88	4.25	0.83	0.28	2.2
P2	3.45	0.84	2.05	0.63	2.73	8.13	4.14	0.70	0.25	1.9
P3	3.50	0.83	3.70	0.63	5.46	7.38	3.79	1.08	0.22	2.1
P4	2.80	0.71	0.88	0.48	0.75	7.88	4.58	0.50	0.29	1.3
P5	4.55	1.10	2.90	0.76	4.74	7.88	4.13	1.75	0.30	1.6
S1	2.65	0.74	0.98	0.46	0.49	10.75	2.63	0.23	0.21	0.6
S2[a]	4.20	1.00	1.10	0.55	0.40	15.00	1.10	0.20	0.17	—
S3[a]	15.60	4.55	20.00	1.50	37.50	25.50	3.10	5.80	0.25	—
S4[a]	4.80	1.05	1.10	0.45	0.40	15.00	1.40	0.60	0.16	—
S5[a]	16.00	4.60	23.00	1.60	42.50	34.50	2.90	3.40	0.26	—
S6	2.60	0.75	0.73	0.41	0.49	11.30	1.39	0.20	0.18	0.3
S7	2.87	1.00	0.97	0.55	0.55	12.50	3.40	0.23	0.20	1.6

[a]1978 mean, $N = 2$.
[b]1978 single sample.

factor incorporating VOL, might do a better job of predicting $THERM_z$. This is not the case ($r^2 = 0.35$). As noted previously, the projection of the PCA of morphometry (Fig. 3) is not typologically unequivocal. However, a comparison of the positions of the lakes suggests that there is a relationship between their position, the developmental pattern of thermal stratification in the lakes (Fig. 2) and the value of $THERM_z$ itself that has a bearing on the applicability of the Ragotzkie model.

The LEWG lake set exhibits four characteristic stratification patterns, named for the type cases of Fig. 2. (1) In the P1 pattern, hypolimnetic waters do not warm above 4°C and the thermocline depth remains constant (±0.5 m) across the summer period (June–August). For our purposes, "summer" stratification ends with the cycle exhibiting significant epilimnial cooling; this definition avoids ambiguities in the determination of $THERM_z$ associated with progressive erosion of the thermocline in the fall. (2) In the K3 pattern, hypolimnetic temperatures do not warm above 4°C but the thermocline moves progressively deeper (>1.0 m) into the water column (i.e. epilimnial thickness increases) across the summer. (3) In the M4–O5 pattern both hypolimnetic temperatures and epilimnial thickness progressively increase. Two examples of this pattern are shown in Fig. 2, since it covers the widest range of lake depths. (4) The O1 group is polymictic.

The P1 pattern lakes (M5, P1, P2, P3, P4, and S7) all have positive factor 1 scores, i.e. they tend to be on the right in Fig. 3. This lake group has the deepest $THERM_z$ (8–12 m, mean = 9.5) as well as generally having the largest surface areas (mean = 5.4 km^2) and volumes (mean = 81.5 × 10^{-3} km^3). Mean depths average 11.9 m. It might be argued that from its position in Fig. 3 alone, Lake O2 belongs with this group; however, on the basis of stratification pattern it would be omitted. The K3 pattern lakes (K2, K3, K5, P5, and S6) have intermediate factor 1 scores and low factor 2 scores. $THERM_z$ in this group ranges from 6 to 12 m with a mean of

TABLE 3. Means and ranges in nutrient concentrations (1980, $N = 8$) for less conservative elements in the LEWG lake set.

Code	Concentration ($\mu g \cdot L^{-1}$)						Conductivity ($\mu S \cdot cm^{-1}$)	pH (vol. wt.)
	Fe	Mn	Si	NH_4	$NO_3 + NO_2$	TP		
K1[a]	20	18	—	—	5	12	157[c]	8.06[c]
K2	200	10	900	24	206	6	163	7.35
	(40–630)	(9–13)	(750–1000)	(21–32)	(5–1500)	(3–9)		
K3	40	15	525	23	11	9	169	7.41
	(20–90)	(9–320)	(250–1850)	(16–40)	(5–40)	(4–20)		
K4[a]	20	19	2150[b]	4[b]	5	9	120[c]	8.30[c]
K5	30	11	687	16	12	5	171	7.52
	(10–40)	(6–16)	(400–1350)	(14–32)	(5–50)	(3–6)		
K6	47	16	1156	36	55	10	155	7.38
	(30–100)	(13–19)	(1000–1600)	(18–60)	(14–290)	(6–14)		
M1	52	21	437	23	33	5	27	5.79
	(20–100)	(7–48)	(250–850)	(16–25)	(5–155)	(4–9)		
M2	43	8	200	15	33	5	27	5.99
	(10–90)	(5–12)	(100–300)	(8–30)	(5–186)	(3–7)		
M3	287	45	556	27	35	12	34	5.79
	(170–430)	(17–66)	(150–1300)	(10–33)	(5–133)	(9–21)		
M4	145	28	787	16	52	9	28	5.07
	(40–210)	(9–45)	(550)–1150)	(10–25)	(10–140)	(5–12)		
M5	32	8	994	21	87	4	50	6.54
	(20–50)	(4–19)	(700–1650)	(18–27)	(15–265)	(2–7)		
M6	42	47	319	19	22	5	23	5.58
	(20–100)	(36–61)	(200–800)	(14–32)	(5–75)	(3–7)		
M7[a]	10	6	450[b]	37[b]	—[c]	1	20[c]	6.90[c]
M8	105	24	744	19	32	12	54	6.60
	(30–220)	(6–60)	(450–1950)	(14–21)	(5–155)	(8–16)		
M9[a]	30	8	1250[b]	65[b]	72	5	20.0[c]	6.50[c]
N1	60[b]	140[b]	1100[b]	30[b]	5[b]	3[b]	20[c]	6.10[c]
N2[a]	20	17	900[b]	54[b]	5	4	30[c]	6.20[c]
N3[a]	20	17	220[b]	44[b]	11	10	30[c]	6.30[c]
N4	222	91	1250	27	35	11	34	5.16
	(150–340)	(83–112)	(1050–1700)	(14–38)	(5–145)	(4–15)		
N5	62	20	1137	23	20	7	32	6.12
	(40–100)	(11–41)	(850–1500)	(10–42)	(5–75)	(5–15)		
O1	45	9	3581	44	12	13	265	8.12
	(30–60)	(96–12)	(3250–4450)	(17–72)	(5–29)	(7–21)		
O2	40	17	1550	25	24	6	188	8.00
	(10–30)	(6–38)	(1400–1750)	(12–37)	(5–40)	(4–10)		
O3	50	17	2869	62	22	18	214	7.99
	(20–80)	(5–26)	(600–6030)	(24–104)	(5–110)	(15–23)		
O4	27	18	2987	61	22	11	276	8.27
	(20–40)	(8–23)	(600–13 000)	(40–84)	(5–95)	(7–16)		
O5	37	19	1562	46	19	14	207	8.09
	(30–40)	(15–27)	(300–8050)	(36–62)	(5–80)	(8–21)		
P1	40	10	606	23	115	6	36	5.87
	(20–60)	(5–20)	(250–1150)	(18–44)	(5–250)	(1–12)		
P2	40	14	606	21	104	4	30	6.05
	(10–60)	(5–36)	(200–1150)	(14–34)	(5–235)	(1–8)		
P3	62	14	512	13	45	4	47	6.19
	(20–110)	(6–31)	(250–900)	(8–20)	(5–140)	(1–8)		
P4	37	16	644	16	45	6	30	6.28
	(10–70)	(5–41)	(450–1000)	(4–34)	(5–135)	(3–10)		
P5	32	10	194	11	9	7	48	6.35
	(10–60)	(5–19)	(50–600)	(2–18)	(5–40)	(3–13)		
S1	70	78	912	31	108	3	36	4.61
	(20–150)	(76–84)	(650–1200)	(20–60)	(15–180)	(1–5)		
S2[a]	10	28	500[b]	43[b]	5	1	35[c]	5.50[c]
S3[a]	20	11	1700[b]	100[b]	5	6	180[c]	7.60[c]
S4[a]	10	15	600[b]	30[b]	5	5	40[c]	6.20[c]
S5[a]	20	7	750[b]	44[b]	5	3	190[c]	6.90[c]

TABLE 3. (*Concluded*).

Code	Concentration ($\mu g \cdot L^{-1}$)						Conductivity ($\mu S \cdot cm^{-1}$)	pH (vol. wt.)
	Fe	Mn	Si	NH_4	$NO_3 + NO_2$	TP		
S6	32 (10–60)	143 (133–160)	1131 (1050–1200)	27 (18–35)	124 (47–155)	3 (1–5)	34	4.57
S7	63 (40–150)	107 (102–116)	1121 (950–1450)	19 (6–44)	48 (5–110)	5 (1–10)	42	4.73

[a]1978 mean, $N = 2$.
[b]1979 spring overturn single sample.
[c]1 m below surface.

8.2 m. These lakes have mean depths similar to the P1-type lakes (mean = 11.8 m) and are not substantially shallower, z_{max} averaging 30 vs. 37 m. However, their surface areas are considerably smaller (mean = 1.2 km^2). The M4–O5-type lakes (K6, M2, M4, M6, M8, N5, O2, O5, and S1) tend to lie even farther to the left in Fig. 3. This group has even shallower $THERM_z$ (mean = 7.8 m) than the first two groups, slightly larger surface areas in comparison with the K3 group (average = 1.7 km^2), slightly smaller volumes (mean = 9.2×10^{-3} km^3), and consequently, smaller mean depths (mean = 6.5 m). While it might be argued that M6, M2, M4, and O5 lie in a region of factor space similar to K2, K3, and P5, the former lakes (arbitrarily) have lower factor 1 scores and higher factor 1 to factor 2 ratios. The scale of the projection is controlled by the structure of the data set. Therefore, although positions shift somewhat, these two groups can be more widely separated yet maintain group membership if the analysis is rerun without S7, M8, and O3. In contrast, the polymictic group (O1, O3, O4, and N4) tends to have low factor 1 scores and high factor 2 scores although N4 appears a bit out of position by factor scope criterion alone. These lakes' surface areas are larger than either the K3 group or the M4–O5 group (mean = 2.5 km^2), volumes are smaller (mean = 6.1×10^{-3} km^3), and mean depths are subsequently smaller (mean = 2 m).

Using Fig. 2 and 3 as the basis for a typological scheme, $THERM_z$ is only significantly predicted by FETCH ($r^2 = 0.83$) or $4\sqrt{FETCH}$ ($r^2 = 0.85$) in those lakes displaying P1-type stratification patterns. The latter equation overall is slightly different from that of Ragotzkie: $THERM_z = 3\sqrt{FETCH} + 0.5$. However, across the ranges of FETCH exhibited by the LEWG lakes, the two equations are virtually indistinguishable. It would be useful to establish some criteria for the application of the Ragotzkie model. It may have been derived from lakes with larger fetches than our data set, although the graphical representation of the model shows some points within the fetch ranges of our systems. Aspects of the basin formation mechanisms of the smaller lakes in the Ragotzkie lake set may differ from ours, leading to different morphometric interrelationships (Kent and Wong 1982). They may, for example, have larger volumes for smaller fetches and/or all exhibit P1-type stratification. We are currently unable to confirm or reject this hypothesis. The tentative conclusion for our data set is that the Ragotzkie model applies only to systems above some critical volume. Below this "critical" volume, morphological factors other than FETCH appear to be more important in the determination of $THERM_z$. For example, while FETCH or $4\sqrt{FETCH}$ will predict $THERM_z$ in the K3 group lakes (see below), VOL does a better job, while score on factor 1 is even better:

$$THERM_z = 0.21FETCH + 0.19, \quad r^2 = 0.43$$

$$THERM_z = 5.0\sqrt{FETCH} + 1.18, \quad r^2 = 0.34$$

$$THERM_z = 0.20VOL + 5.14, \quad r^2 = 0.56$$

$$THERM_z = 0.07PC\text{-}1 - 0.49, \quad r^2 = 0.61.$$

In the M4–O5 lakes there is no relationship between $THERM_z$ and either FETCH or $4\sqrt{FETCH}$. Volume shows a weak trend ($r^2 = 0.31$) with $THERM_z$. Position on factor 1 is the only significant predictor ($P < 0.05$) of $THERM_z$ ($THERM_z = 0.14PC\text{-}1 - 1.27$, $r^2 = 0.58$).

The argument may be made that a lake's score on PCA will be dependent on the mix of lakes in the analysis, and hence, predictions based on it will lack general applicability. We do not totally disagree with that argument but tend to view PCA as a hypothesis-generating mechanism. PCA represents a linear combination of the variables that go into it, and the factors that come out are reasonably interpretable. Therefore, a combination of standard morphometric variables should exist that will function almost equally well (in terms of explanatory power) as factor scores. In addition, although a particular PCA may be unique to the data set from which it emerged, the predictive ability of the composite standard morphometric variable that comes from it should have a wider applicability than the factor score.

An example can be drawn from the work of Gates et al. (1983) on the interpretation of year-to-year variations in the trajectories of 16 size classes of planktonic biomass. A summary variable for one axis of trajectory movement was the ratio of nannoplankton to filter-feeding zooplankton. Mean position on this axis was attributed to aspects of lake morphometry, as 44% of the variance in mean position was accounted for by lake volume alone. Figure 5 summarizes the nannoplankton to filter-feeding zooplankton ratios (NAN PL/FF ZOO) as a function of net plankton (NET PL) biomass. It is clear that there is a fairly strong relationship between at least five of the six P1 type stratification pattern lakes (P1, P2, P4, S7, and M5) and high NAN PL/FF ZOO ratio. Alternatively, the M4–O5 lakes tend to have low NAN PL/FF ZOO ratios. While gross division of the plankton community into four compartments may be a less than adequate characterization of community structure (Gates et al.

TABLE 4. Complete morphometric data set correlation matrix.

	$\bar{z}$	z_{max}	AREA	VOL	PERIM	D_L	REL_z	$\bar{z}:z_{max}$	LITT	$THERM_z$	EPI_z	A_{sol}	LITE	V_{epi}	FETCH	Ae/Ve
$\bar{z}$	1.00															
z_{max}	0.92	1.00														
AREA	0.11	0.27	1.00													
VOL	0.56	0.68	0.81	1.00												
PERIM	0.29	0.49	0.83	0.85	1.00											
D_L	0.28	0.45	0.69	0.65	0.90	1.00										
REL_z	0.67	0.60	−0.43	−0.06	−0.20	−0.13	1.00									
$\bar{z}:z_{max}$	0.18	−0.20	−0.43	−0.27	−0.48	−0.43	0.21	1.00								
LITT	−0.70	−0.75	−0.16	−0.52	−0.41	−0.32	−0.55	0.12	1.00							
$THERM_z$	0.76	0.64	0.19	0.43	0.27	0.31	0.44	0.32	−0.44	1.00						
EPI_z	0.56	0.42	0.26	0.37	0.26	0.31	0.22	0.36	−0.36	0.88	1.00					
A_{sol}	−0.21	−0.13	0.71	0.26	0.36	0.46	−0.49	−0.30	0.25	0.03	0.21	1.00				
LITE	−0.07	−0.27	−0.43	−0.42	−0.43	−0.43	0.17	0.37	0.39	−0.14	−0.24	−0.37	1.00			
V_{epi}	0.41	0.52	0.88	0.94	0.84	0.65	−0.20	−0.24	−0.44	0.48	0.50	0.41	−0.49	1.00		
FETCH	0.31	0.44	0.68	0.77	0.72	0.52	−0.21	−0.31	−0.22	0.28	0.19	0.17	−0.12	0.74	1.00	
Ae/Ve	−0.61	−0.57	−0.04	−0.31	−0.22	−0.24	−0.53	−0.25	0.57	−0.66	−0.53	−0.20	0.13	−0.28	−0.12	1.00

1983; B. Holtby, G. W. Sprules, H. H. Harvey, and A. P. Zimmerman, unpublished data), we feel we have taken a step in the process of moving from a multivariate, potentially lake set specific explanation of data to extraction of appropriate combinations of morphological variables with the use of the multiple linear regression analysis presented in Table 6. Mean depth to maximum depth ratio ($\bar{z}:z_{max}$), a good correlate of PC-2, and volume (VOL), a good correlate of PC-1, are two of the most important variables for explaining variance in NAN PL/FF ZOO ratio, $R^2 = 0.91$, an improvement of 47% over the explanation of that variable presented in Gates et al. (1983).

CHEMICAL ANALYSES

In the previous section we showed that for the LEWG data set as a whole a PCA-derived morphometric variable can explain a greater percent variance than a standard morphometric variable in several regression-based models. A typology derived in part from PCA was useful in identifying groups of lakes for which a particular model was appropriate and other groups of lakes that appear to be bona fide outliers. In addition, variables important in defining the typology were shown to be among the most important in a stepwise multiple linear regression explaining nannoplankton to filter-feeding zooplankton relationships among the lakes. However, the lake "types" derived from the analysis did not provide any additional insights into lake behavior when the dependent variable of interest was chlorophyll. We suggested that this was at least partly due to the influence of variables not considered in the analysis, in this case, lake chemistry. Given this latter result, we were interested in whether lake chemical relationships, in particular a speciated chemical matrix, would be able to function similarly to morphometry. Specifically, could a multivariate approach to system chemistry produce better predictive variables, more useful combinations of standard chemical variables, or provide a basis for a chemical typological scheme, and would standard regression equations provide better predictions within these types?

The results of PCA run on the total analytical concentrations of elements from Tables 2 and 3 are presented in Fig. 6a. Eigenvalues, percent variance explained, and loadings for the first two factors are given in Table 7. Factor 1 in Fig. 6a is primarily a contrast between pH ($r = -0.93$) and pCO_3 ($r = 0.92$). Factor 2 is related to the relative concentrations of silica, ammonia, and manganese in the lakes. As might be expected from an analysis using total analytical concentrations of elements, the major factor accounting for differences in system chemistry between the LEWG lakes is location on or off the Precambrian Shield.

The Orillia (O) lakes are primarily off the shield on limestone−dolostone formations, although O2 and O5 have portions of their watersheds in igneous formations. Consequently, the O lakes exhibit the highest ionic strength among the lake groups. Their major inorganic anions balance the major cations and their anion composition is dominated by carbonates (Fig. 7). The systems are well buffered and pH's are high. The Kawartha (K) lakes are on the Shield boundary. They have carbonate-containing formations in their watersheds, but these are not limestones per se. There is little evidence of significant dolostone formations in the area and

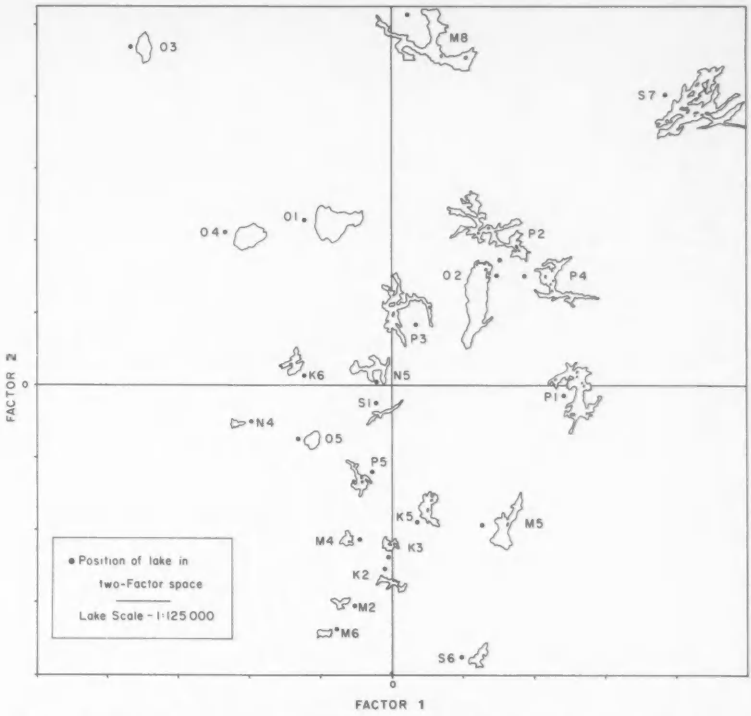

FIG. 3. Projections of scores from principal components analysis of morphometric data set into two-dimensional factor space along with scaled outlines of the lakes.

TABLE 5. Eigenvalues, % variance explained, and factor loadings for morphometric PCA.

	Factor 1	Factor 2
Eigenvalue	7.58	4.52
% variance explained	42.12	25.10
Loadings		
$\bar{z}$	0.75	−0.47
z_{max}	0.83	−0.25
AREA	0.63	0.72
VOL	0.85	0.36
PERIM	0.76	0.54
D_L	0.70	0.45
REL_z	0.27	−0.80
$\bar{z}:z_{max}$	−0.14	−0.61
LITT	−0.70	0.30
$THERM_z$	0.74	−0.42
EPI_z	0.66	−0.27
A_{sed}	0.19	0.65
LITE	−0.44	−0.34
V_{epi}	0.83	0.44
FETCH	0.61	0.43
Ae/Ve	−0.67	0.58

calcium accounts for a much higher percentage of total cations than in the O lakes. Ionic strength is reduced relative to the O lakes, but inorganic anions and cations still balance, and carbonates still make up the majority of the anion pool. The lakes are reasonably well buffered with pH's usually above 7.

The Muskoka (M), North Bay (N), Parry Sound (P), and Sudbury (S) lakes are all located on the Shield. Their ionic strength is concomitantly reduced and all appear to have a component of major anion missing. A portion of the missing anionic budget can probably be accounted for by the presence of refractory organic compounds (primarily humic and fulvic acids). However, the difficulty in equating a specific humic–fulvic concentration with some number of equivalents makes this aspect of system chemistry difficult to quantify. An alternative explanation is that the systems are not deficient in anions but have artificially high cation equivalent sums. In the absence of ion exchange data this alternative is equally difficult to assess but could result from increases in the importance of hydrated and/or polymerized metal species whose actual charges are less than expected.

Sulfate is either equal to or dominates the major inorganic anions in three of the four shield lake groups. The P lakes are an exception. They show a large Cl^- (and Na^+) component, possibly due to halides associated with the metavolcanic deposits in the area. Buffering is low to negative in all the Shield lakes. The pH is reduced, particularly in the spring (Fig. 2). As such, the primary picture from Fig. 6a is similar to that of Fig. 7: the O lakes with the highest inorganic carbon contents and highest pH's (lowest hydrogen ion

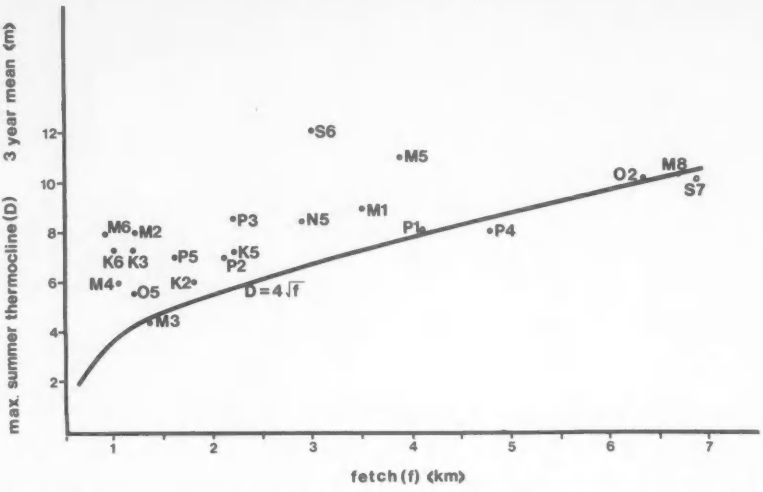

FIG. 4. Relationship between $THERM_z$ and FETCH in the LEWG data set and its relationship to the Ragotzkie model.

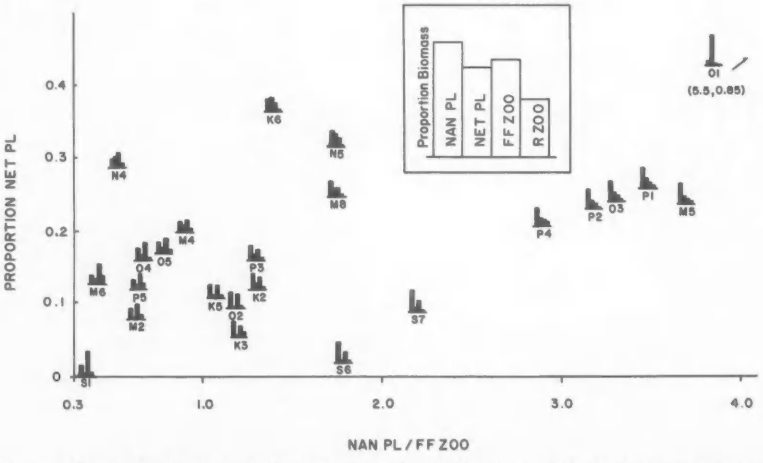

FIG. 5. Distribution of pelagic planktonic biomass in the LEWG lakes as defined by the nannoplankton to filter-feeding zooplankton ratio (NAN PL/FF ZOO) and the proportion of planktonic biomass in netplankton (NET PL).

TABLE 6. Summary table from stepwise multiple linear regression of NAN PL/FF ZOO on morphometric variables.

Variable	multiple R^2	r^2	B
$\bar{z}:z_{max}$	0.61	0.38	−39.34
LITE	0.77	0.60	0.33
VOL	0.85	0.72	124.00
A_{sed}	0.87	0.72	0.68
AREA	0.91	0.83	−1.92
Constant			12.11

concentrations) contrasted with the S lakes.

Many of the elements important in this initial chemical PCA are highly chemically active undergoing either complexation−coordination, acid−base, or redox reactions. The particular matrix of chemical species present in a given lake can have a profound effect on the distribution and availability of nutrients in that system with subsequent implications for the lake's biological structure. We therefore felt it was important to attempt an assessment of the impact of speciation for system chemistry. Our initial effort has been to use REDEQL-II, a chemical equilibrium computer program.

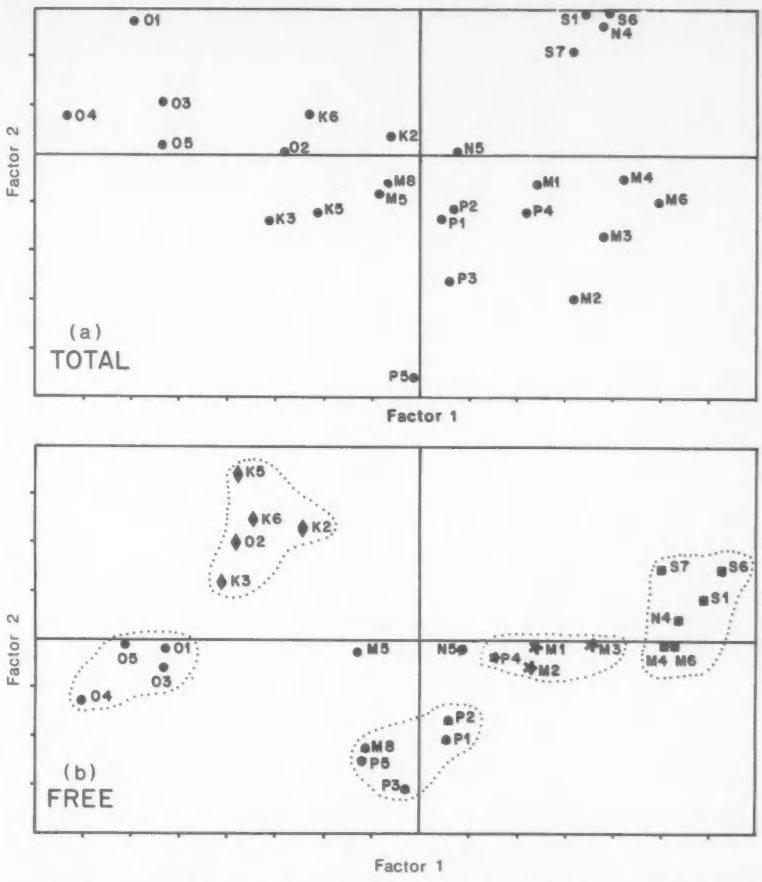

FIG. 6. Projection of PCA of (a) total and (b) REDEQL-II predicted "free" nutrient concentrations into two-factor space.

Using the total analytical concentration of metals and ligands, the proton and electron intensities, and the ionic strength in each system, plus gas partial pressures and extensive thermodynamic data, REDEQL-II iteratively arrives at the equilibrium distribution of solid, complexed, and "free" or aquo-phases for the particular lake. Analytical tools sufficiently precise to identify all the chemical forms are lacking, average epilimnetic chemical conditions cannot capture the dynamic patchiness (Richerson et al. 1970) of the trophogenic zone, and it is debatable as to whether any natural water system is ever at equilibrium. Consequently, it is an arbitrary process to select a particular chemical species and suggest that it may be more "biologically available" than another. Nevertheless, having to start somewhere, we have chosen the "free" species as being more representative of the available chemical matrix and as the basis of a second PCA. The projection of this latter analysis is shown in Fig. 6b. Eigenvalues, percent explained variance, and loadings are presented in Table 7. Despite our uncertainty as to the analytical interpretation of "free species" and questions as to whether the free pool is the appropriate pool to use, the variance explained in the REDEQL-II based PCA is better than that from the total analytical concentration PCA (77.7 vs. 63.4%) and the factors appear to be more interpretable. Hydrogen ion concentration remains an important component of factor 1, but it is now contrasted with a suite of biologically active elements (H_xPO_4, NH_x, Fe^{3+}, H_xCO_3, SiO_3). Factor 2 consists primarily of more conservative elements (Na, Cl, SO_4). In addition, Fig. 6b suggests a visually cleaner separation of the lakes into groups. While Fig. 6 represents the analyses of the 1980 chemical matrices, similar analyses of the 1979 data indicate that the groups remain stable. Loadings and factor scores differ somewhat; however, only M2 moves out of its group to assume a solitary position.

There are several observations that suggest that aspects of chemical speciation provide a useful perspective against

TABLE 7. Eigenvalues, % variance explained, and loadings for PCA on both total analytical concentrations (TOT CONC) and REDEQL-II predicted "free" concentrations (FREE) from LEWG lake set chemistry.

	TOT CONC		FREE	
	Factor 1	Factor 2	Factor 1	Factor 2
Eigenvalue	6.697	2.043	9.458	1.425
% variance explained	47.83	14.59	67.56	10.18
Loadings				
Ca	0.892	−0.108	0.826	−0.485
Mg	0.698	0.093	0.700	−0.269
K	0.883	−0.039	0.842	0.067
Na	0.667	0.173	0.595	0.651
Fe^{3+}	−0.420	−0.363	−0.987	0.037
Mn^{2+}	−0.516	−0.669	−0.720	−0.211
$CO_3 + HCO_3$	0.921	−0.490	0.982	−0.062
SO_4	0.557	−0.498	0.355	−0.564
Cl	0.752	0.307	0.742	0.557
NH_4	0.649	−0.633	0.982	−0.059
PO_4	0.389	−0.181	0.980	0.002
SiO_3	0.603	−0.696	0.985	−0.067
NO_3	−0.478	−0.320	−0.477	−0.056
pH	−0.926	−0.219	−0.987	0.038

which to view biological patterns in lakes. Figure 8 details the relationship of total phosphorus to chlorophyll, total phytoplankton biomass, netplankton biomass, and nannoplankton biomass for the LEWG lakes. For the phosphorus–chlorophyll panel, two alternative models are also shown: Chl $a = 40.1/(1 + 130.1 \exp(-1.14TP))$ (Straskraba 1980) and Chl $a = 0.0731TP^{1.45}$ (derived from Dillon and Rigler 1974 by Straskraba 1980). Perhaps due to similar methodology or because the LEWG lakes are generally low in total phosphorus and in similar geological and land use categories as the lakes used by Dillon and Rigler, the second model is a better fit to the data ($r^2 = 0.61$) than the first ($r^2 = 0.31$) and almost as good as the linear model generated from the LEWG data itself ($r^2 = 0.68$). In all cases, explained variance decreases when wet weight biomass is substituted for chlorophyll. There is a reasonably consistent relationship between groupings in Fig. 6b and position on the phosphorus–nannoplankton panel of Fig. 8, suggesting that within-typology analyses might prove useful. For example, K2, K3, K5, K6, and O2 from Fig. 6b all fall above the regression line in Fig. 8 and M4, M6, N4, S1, S6, and S7 all fall below the line. Interestingly, the former group has the higher phosphorus concentrations and higher percent "free" phosphorus (55 vs. 41%). This tends to support the Golterman and Kouwe (1980) contention that the increasing return to scale of the phosphorus–phytoplankton biomass relationship can be explained on the basis of lower availability at lower concentrations (or more efficient recycling at higher concentrations).

If groups are formed rather arbitrarily as outlined in Fig. 6b and the phosphorus–phytoplankton biomass relationships are reanalyzed (Table 8), a higher percent of the variance in biomass is usually explained within the groups for total biomass, net plankton biomass, and nannoplankton biomass than is explained across the data set as a whole. The results are mixed for chlorophyll. Although an increased amount of variance is explained using within-type analyses, the relationship between groupings in Fig. 6 and outlier status in Fig. 8 is clearest for the phosphorus–nannoplankton relationship, suggesting that P availability may be less important for net plankton population dynamics and hence for total plankton when net plankton constitute a high proportion of the total.

Just as chemistry influenced the morphometric-based analysis of chlorophyll relationships presented in the preceding section, feedback from the biological community appears to add an additional layer of complexity to chemical–phytoplankton relationships. In the phosphorus–nannoplankton regression from Fig. 8, for example, systems with a low NAN PL/FF ZOO ratio (circled lakes) fall below the regression line (i.e. have less nannoplankton biomass than might be expected for a given total phosphorus concentration) at low values of phosphorus, while occurring above the regression at higher phosphorus values. Paloheimo and Zimmerman (1983) reported that taking the effect of filter-feeding zooplankton into account improved the prediction of phosphorus–nannoplankton relationships. However, for the LEWG lake set as a whole, the improvement in explained variance amounted to only about 10%. Results presented here suggest that the improvement might have been more substantial if the effect of grazers had been investigated within as well as across their biologically defined lake types.

In contrast with the morphometric typology–chlorophyll relationship, neither REDEQL-II predicted "free" phosphorus nor score on factor 1 explained more variance in plankton biomass than total phosphorus alone, either within groups or across the data set as a whole.

General Discussion

One of the central problems in ecology is how to describe ecosystems in a parsimonious yet functionally adequate manner (Paloheimo et al. 1983). The situation is compounded in the pelagic ecosystem not only by increased trophic complexity but by genuine uncertainty as to whether resource–

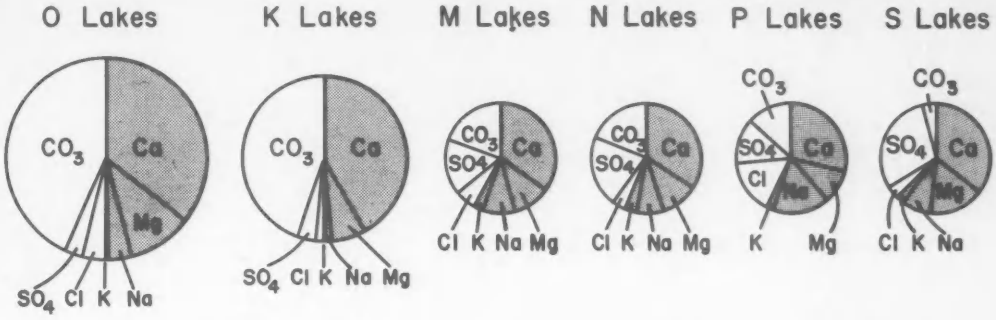

FIG. 7. Relative proportions of Ca, Mg, Na, K, CO_3, SO_4, and Cl in the O, K, M, N, P, and S lakes (circle diameter is proportional to system ionic strength).

TABLE 8. Equations (not reported for nonsignificant r^2) and % variance explained for within-type analyses of total phosphorus to phytoplankton biomass (* = $P < 0.10$, ** = $P < 0.05$, *** = $P < 0.01$, NS = not significant).

Lake group	Dependent variable	Slope	Intercept	r^2	P
O1, O3, O4, O5	NANNO PL	**	**	0.23	NS
K2, K3, K5, K6, O2	NANNO PL	48.7	274	0.94	**
P1, P2, P3, P5, M8	NANNO PL	76.7	131	0.66	*
M1, M2, M3, P4	NANNO PL	10.3	406	0.55	*
M4, M6, N4, S1, S6, S7	NANNO PL	18.7	280	0.85	**
O1, O3, O4, O5	NET PL	**	**	0.05	NS
K2, K3, K5, K6, O2	NET PL	117	−59.6	0.72	*
P1, P2, P3, P5, M8	NET PL	58.3	−82.5	0.75	*
M1, M2, M3, P4	NET PL	84.0	−24.7	0.98	**
M4, M6, N4, S1, S6, S7	NET PL	68.1	−189	0.69	*
O1, O3, O4, O5	TOT PL	**	**	0.07	NS
K2, K3, K5, K6, O2	TOT PL	59.2	304	0.98	***
P1, P2, P3, P5, M8	TOT PL	134	48.2	0.70	*
M1, M2, M3, P4	TOT PL	94.2	186	0.95	**
M4, M6, N4, S1, S6, S7	TOT PL	76.7	126	0.63	*
O1, O3, O4, O5	CHL	**	**	0.58	NS
K2, K3, K5, K6, O2	CHL	**	**	0.42	NS
P1, P2, P3, P5, M8	CHL	0.72	−2.0	0.75	*
M1, M2, M3, P4	CHL	**	**	0.17	NS
M4, M6, N4, S1, S6, S7	CHL	0.32	−0.19	0.82	**

consumer regressions should be characterized by positive or negative coefficients, i.e. at what levels are pelagic ecosystems under resource or predation control (Weigert and Owen 1971; Hall et al. 1976; Hrbacek 1979; Blazka et al. 1980). Rather than echoing the increasingly familiar lament that the complexity of lake ecosystems will lead inevitably to the failure of dynamic models (Hedgepeth 1977), LEWG has taken the position that both coefficient signs are appropriate in different "types" of lakes and that different models may often be necessary to express functional responses in different lake types.

In this paper we have suggested that multivariate morphometric and chemical analyses are one method of elucidating these lake "types." Both have been shown to be useful here, although not in identical manners. The morphometric PCA did not provide a completely clearcut typology. Nevertheless, there was a reasonably straightforward relationship between factor position and thermal stratification pattern that did yield a typological scheme. Using this scheme, we were able to identify groups of lakes that are outliers for the Ragotzkie model predicting the maximum depth of the summer thermocline. We currently lack sufficient data on the lakes that comprised the original model to allow us to confirm our hypotheses regarding appropriate criteria for use of that model. However, it appears that for lakes in our data set at least, there must be either a sufficiently large volume or critical depth for the model to work. Factor scores from the morphometric PCA were also used in place of fetch to predict

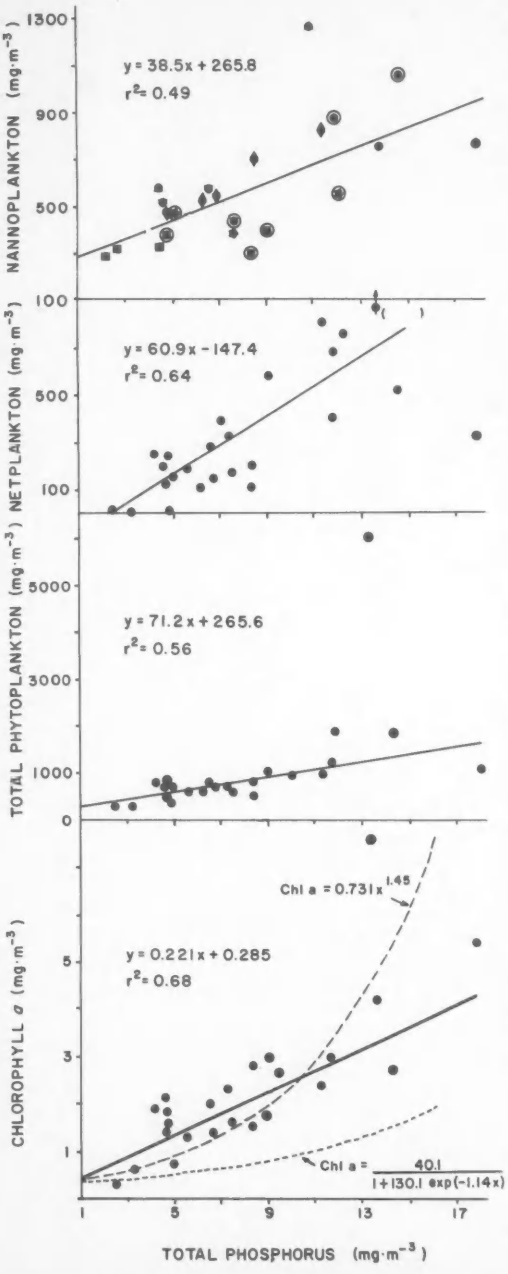

FIG. 8. Relationship of total phosphorus to chlorophyll, total phytoplankton biomass, net plankton biomass, and nannoplankton biomass.

summer thermocline depth or in place of other standard morphometric variables ($\bar{z}$, Ae/Ve) in predictions of lake chlorophyll concentrations. As might be expected for a more information-rich variable, factor scores always explained higher percentages of variance.

A PCA can be criticized as too lake set specific. We have argued that since PCA factors represent interpretable linear combinations of variables, they can play an important role in the illucidation of useful combinations of more standard variables. We have shown that two variables, important in the factor loadings of the morphometric PCA ($\bar{z}$:z_{max} and VOL), plus a variable incorporating the amount of incident light to the thermocline (LITE) will explain 91% of the variance in nannoplankton to filter-feeding zooplankton ratio. In other words, lakes with a reasonable amount of light (more than 10% of incident) at the thermocline are characterized by plankton communities that have the majority of their biomass in nannoplankton. Alternatively, shallower lakes, less well lit to the thermocline, tend to have much higher proportions of filter-feeders in their plankton populations. We suggest that the former lakes are representative of a "type" in which phytoplankton populations will be more resource controlled, with filter-feeding zooplankton densities being a function of predation. We suggest that grazing on the nannoplankton will be a much more important density-regulating mechanism for this trophic level in the latter lake type.

Despite the cleaner typology suggested by the PCA of the speciated chemical matrix, factor scores were not useful in explaining increased amounts of variance for the data set as a whole. In general, however, phosphorus–phytoplankton regressions were better within the chemically defined lake types than across all the lakes. We were most intrigued with suggestions of overlap between chemically and morphologically defined lake types, particularly with regard to density regulation mechanism responses from the biological community. For example, the K2, K3, K5, K6, O2 group from Fig. 6b, appeared above the regression line in the nannoplankton panel of Fig. 8. In other words, they had more nannoplankton biomass than expected for their phosphorus concentration and utilized it relatively effectively (1P: 48.7NAN PL). This group all had nannoplankton to filter-feeding zooplankton ratios greater than 1 (Fig. 5). The M4, M6, N4, S1, S6, S7 group, which appeared below the regression line, i.e. less nannoplankton than expected for the phosphorus concentration, utilized phosphorus less effectively (1P: 18.7NAN PL) and all but S6 and S7 had nannoplankton to filter-feeding zooplankton ratios below 1. We suggest that the first group represents lakes with a higher degree of resource control on the nannoplankton, while the latter group consists of lakes with a greater degree of grazer control.

Not all the lakes can be typed as easily. These two groups may represent ends of a continuum with lakes in the middle under constantly fluctuating density control mechanisms. The models presented here are by no means complete. However, we feel we have demonstrated the utility of a principal components approach to lake physicochemistry, adequately demonstrated the existence of morphometric and chemical lake "types," shown that different models apply within those types, and suggested a continuum of response to physicochemical conditions from the biological community.

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Factors Influencing Phosphorus–Phytoplankton Relationships[1]

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PALOHEIMO, J. E., AND A. P. ZIMMERMAN. 1983. Factors influencing phosphorus–phytoplankton relationships. Can. J. Fish. Aquat. Sci. 40: 1804–1812.

In a set of small Ontario lakes sampled from 1978 to 1981, the correlation between the mean ambient total phosphorus concentration, P, and phytoplankton biomass ranges from $r^2 = 0.29$ to $r^2 = 0.46$. The correlation is somewhat higher between P and nannoplankton corrected for turnover rate than between P and the total phytoplankton or straight nannoplankton biomass. The correlation is affected by the abundance of grazers and by lake morphology. Regressions based on log–log transformed values showed a decreasing return to scale (i.e. biomass increases at a slower rate relative to increases in P) in contrast with many earlier studies. We suggest that a decreasing return to scale is to be expected when primary production, rather than chlorophyll or phytoplankton biomass, is used as the dependent variable. Lakes were clustered on the basis of mean abundance in four functional plankton groups (nannoplankton, net phytoplankton, herbivorous zooplankton, and carnivorous zooplankton), as well as on the basis of water chemistry and watershed geology. Only clusterings based on the structure of the entire plankton community appear to have a real effect on the phosphorus–phytoplankton relationship, showing increasing simple correlations from $r^2 = 0.29$ to $r^2 = 0.41$ within clusters and multiple correlations to $R^2 = 0.97$ overall. These relationships imply that while the typical phosphorus–phytoplankton relationship is generally valid, its specific form depends on the characteristics or "type" of lake ecosystem.

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Dans une série de petits lacs ontariens échantillonnés entre 1978 et 1981, la corrélation entre la teneur ambiante moyenne de phosphore total, P, et la biomasse phytoplanctonique varie de $r^2 = 0{,}29$ à $r^2 = 0{,}46$. La corrélation est un peu plus élevée entre P et le nannoplancton auquel a été appliquée une correction pour tenir compte du taux de renouvellement, d'une part, qu'entre P et le phytoplancton total ou la simple biomasse phytoplanctonique, d'autre part. L'abondance des brouteurs et la morphologie du lac influencent la corrélation. Des régressions fondées sur les valeurs log–log transformées indiquent que les augmentations de biomasse se produisent à un taux décroissant par rapport aux augmentations de P, contrairement aux résultats de plusieurs études antérieures. Il faut s'attendre, croyons-nous, à une telle diminution des taux d'accroissement quand la production primaire, plutôt que la chlorophylle ou la biomasse phytoplanctonique, est utilisée comme variable dépendante. Les lacs furent groupés en fonction de l'abondance moyenne de quatre groupes fonctionnels (nannoplancton, phytoplancton tamisé, zooplancton herbivore et zooplancton carnivore) et aussi en fonction de la composition chimique de l'eau et de la nature géologique du bassin hydrographique. Seuls les groupements fondés sur la structure de la communauté planctonique entière semblent réellement influencer la relation plancton–P, indiquant des corrélations simples qui augmentent de $r^2 = 0{,}29$ à $r^2 = 0{,}41$ au sein des groupes et des corrélations multiples atteignant $R^2 = 0{,}97$ dans l'ensemble. Ceci laisse supposer que, bien que la relation phosphore–phytoplancton typique soit généralement valide, sa forme spécifique dépend du « type » d'écosystème lacustre ou de ses caractéristiques.

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OUR main objective in this paper is to examine the effects of lake morphology, various limnological variables, water chemistry, and the structure of the total planktonic community on the nutrient phytoplankton relationships of a series of Ontario lakes. While the basic phosphorus–phytoplankton relationship has been the subject of numerous papers, only a few of

which are referred to here, we believe that its dependence on the structure of the remaining plankton community or on the system's chemical matrix has not been well demonstrated. Ideally, the nutrient aspect of the relationship would be some measure of loading, which after consideration of mean depth, flushing, etc., would be expressed as a concentration (Vollenweider 1969). In turn, concentrations are then often correlated with the ensuing primary production in the system (e.g. Dillon and Rigler 1974; Sakamoto 1974).

However, there are a number of difficulties in predicting the loading of a nutrient such as phosphorus (P) into an unmetered system, i.e. prediction solely from watershed characteristics and rainfall data. While the amount of nutrient leached from the drainage basin is certainly dependent on the watershed geology, soil type, and land use pattern, published export coefficients still vary over a substantial range of values within each watershed type (Dillon and Kirchner 1975). Similarly, aeolian loading is quite variable and may require on-location measurement in order to achieve a reasonable level of precision (e.g. Schaffner and Oglesby 1978). In addition, the simple one-compartment mass balance equation assumption that lakes are well-mixed reaction vessels is rarely met. The attempts to overcome the uncertainties imposed by this simplification, i.e. loading per mixed volume (Oglesby and Shaffner 1978; Oglesby 1977), loading per outflow (Schindler 1978; Schindler et al. 1978), etc., still assume a reasonably precise estimate of loading.

Consequently, we have chosen to use the mean summer epilimnetic values of P as our independent variable. Mean P can in fact be considered as "effective" loading in the sense that it is a measure of the amount of P received and retained by the epilimnion, corrected both for flushing and sedimentation. Without ignoring the contributions that information on nutrient loading have made to an understanding of trophic relationships in lakes, we feel that our approach allows us to better evaluate the role that morphometry, chemistry, and total plankton community structure play in modifying phosphorus–phytoplankton relationships, without having to deal with the additional uncertainties contributed by imprecise nutrient loading estimates or by the flux of nutrients between lake compartments.

Methods

The data used in this paper come from a set of 25 small Ontario lakes that were sampled between 1978 and 1981 by the Lake Ecosystem Working Group (LEWG) at the University of Toronto. Initially, the lakes (Tables 1 and 2) were chosen to create as diverse a set as possible on the basis of watershed geology, morphometry, and known piscivorous fish community. All of the lakes considered here are within a day's driving distance from Toronto and have essentially one basin. Lakes were sampled at least every fortnight, or eight times from May to September, for physicochemical data, and phytoplankton and zooplankton biomass, at the location of maximum depth. Mean values are thus seasonal means. Each sampling period is referred to as a cycle.

Routine physicochemical data included temperature, pH, pE, conductivity, and dissolved oxygen. These were determined at 1-m intervals using a HydroLab surveyor (HydroLab Corp., Austin, TX), with less frequent measurements at greater depths in the hypolimnion. Water samples intended for chemical analyses were collected twice in 1978, four times in 1979, and eight times in 1980 and 1981. Collection was made using an integrated 4-m tube. Analyses were performed with standard chemical techniques (Ontario Ministry of the Environment 1981) at the laboratories of the Ontario Ministry of the Environment, Rexdale, Ont. In addition to total concentrations as measured above, free, complexed, and solid phases of each of the chemical elements were determined with the aid ot the chemical equilibrium computer program REDEQL-II (McDuff and Morel 1973). In contrast with the total analytical concentrations of metals and ligands, we considered the REDEQL-II transformed chemical "free" species to be a closer reflection of the chemical matrix actually available to the plankton community.

Phytoplankton were also sampled using a 4-m tube. Lugol's preserved samples were settled for 24 h and enumerated and sized with an ocular micrometer. Biomasses were calculated from standard geometric formulae and expressed in five size classes based on equivalent spherical diameters; filamentous algae were placed in a separate category (Sprules and Knoechel 1983). Zooplankton samples were collected with a near-bottom to surface tow using a 110-μm mesh Wisconsin net equipped with a flowmeter. Subsamples of alcohol-preserved zooplankton were placed in a circular counting chamber and projected onto a screen where individuals were sized into one of five classes and categorized as either herbivores or carnivores. Conversion from numbers to wet weight biomass was made (Sprules and Holtby 1979) using the length–weight curves of Hillbricht-Ilkowska and Patalas (1967).

Morphometric data and bathymetric maps were supplied by the Ontario Ministry of the Environment and the Ontario Ministry of Natural Resources. Watershed area and percentage of watershed in each geological category were determined by planimetry of the 1:50 000 scale topographic maps (3rd ed., Energy Mines and Resources Canada) and the 1:250 000 Geological Compilation Series Maps (Ontario Ministry of Natural Resources), respectively. Flushing rate calculations were based on long-term average areal runoff, precipitation, and evaporation (Pentland 1968).

The Statistical Analysis System's (SAS Institute Inc. 1981) Fastclus procedure was used to cluster the lakes into disjoint sets or lake "types." This clustering procedure is based on Euclidean distances computed for those attributes used to characterize the lakes. In addition, simple linear regression and multiple squared correlation analyses (SAS Institute Inc. 1981) were used to analyze the variance associated with selected aspects of the lakes' morphometry, chemistry, and biology. The list of all of the variables used in this study is shown in Table 3.

Results

Phosphorus versus Phytoplankton Biomass

As expected, mean epilimnetic P concentration varies during the season. The observed mean P for all 3 yr has been taken as representative of the actual seasonal mean P,

TABLE 1. Lake names, codes, locations, approximate watershed geologies, and years sampled.

Name	Code	Location		Watershed geology	Year sampled			
		Lat.	Long.		1978	1979	1980	1981
Bass	K1	44°41′	78°32′	Mixed carbonate, conglomerate, felsic, nephaline	×			
Fortescue	K2	44°50′	78°26′	70% carbonate, 15% conglomerate, 15% nephaline	×	×	×	
Picard	K3	44°47′	78°23′	88% carbonate, 6% conglomerate, 6% nephaline	×	×	×	
Salerno	K4	44°51′	72°29′	Mixed carbonate, conglomerate, felsic, nephaline	×			
Salmon	K5	44°59′	78°27′	90% carbonate, 10% conglomerate	×	×	×	
White	K6	44°50′	78°29′	100% carbonate	×	×	×	×
Bigwind	M1	45°03′	79°03′	100% conglomerate	×	×	×	
Blue Chalk	M2	45°12′	78°56′	100% conglomerate	×	×	×	×
Brady	M3	45°03′	78°50′	100% conglomerate	×	×	×	
Crosson	M4	45°05′	79°02′	100% conglomerate	×	×	×	×
Mountain	M5	45°59′	78°43′	65% conglomerate, 20% anorthosite, 15% carbonate	×	×	×	×
Plastic	M6	45°11′	78°50′	100% conglomerate	×	×	×	×
Solitaire	M7	45°23′	79°01′	100% conglomerate	×			
Three Mile	M8	45°10′	79°27′	100% conglomerate	×	×	×	×
Tock	M9	45°16′	78°56′	100% conglomerate	×			
Bacon	N1	45°53′	79°21′	100% felsics	×			
Eagle	N2	45°50′	79°30′	100% felsics	×			
Forest	N3	45°49′	79°18′	100% felsics	×			
King	N4	45°53′	79°30′	100% felsic	×	×	×	×
Ruth	N5	46°01′	79°31′	100% felsic	×	×	×	×
Bass	O1	44°36′	79°30′	100% limestone	×	×	×	
Four Mile	O2	44°41′	78°45′	34% limestone, 66% conglomerate	×	×	×	
Mud	O3	44°40′	79°18′	100% limestone	×	×	×	
Orr	O4	44°36′	79°10′	100% limestone	×	×	×	
Young	O5	44°43′	79°10′	66% limestone, 34% conglomerate	×	×	×	×
Blackstone	P1	45°14′	79°53′	30% conglomerate, 70% anorthosite	×	×	×	
Crane	P2	45°13′	79°57′	25% conglomerate, 25% metavolcanic, 50% anorthosite	×	×	×	
Horseshoe	P3	45°18′	79°51′	30% conglomerate, 70% metavolcanic	×	×	×	
Otter	P4	45°17′	79°58′	100% metavolcanic	×	×	×	
Rankin	P5	45°18′	79°54′	10% conglomerate	×	×	×	
Carlyle	S1	46°04′	81°17′	50% quartzite, 50% felsic	×	×	×	
Joe	S2	46°44′	81°17′	Mixed felsics, various iron formations	×			
McFarlane	S3	46°25′	80°59′	Mixed carbonates and mafics	×			
Nelson	S4	46°44′	81°05′	Mixed felsics, various iron formations	×			
Ramsey	S5	46°29′	80°57′	Mixed carbonates and mafics	×			
George	S6	46°02′	81°24′	80% quartzite, 20% felsic	×	×	×	
Tyson	S7	46°07′	81°07′	60% conglomerate, 40% felsic	×	×	×	

TABLE 2. Lake morphometry.

Lake code	Drainage area (km^2)	Flushing rate (yr^{-1})	Lake area (km^2)	Mean depth (m)	Maximum depth (m)	Volume ($km^3 \times 10^{-3}$)	Perimeter (km)
K1	130.00	9.88	1.15	4.3	9.8	5.0	8.3
K2	35.03	1.43	0.79	11.8	28.7	9.3	9.3
K3	9.32	0.45	0.76	10.2	35.1	7.7	5.9
K4	67.89	2.80	1.45	6.3	13.4	9.0	13.2
K5	5.63	0.11	1.72	11.3	30.5	19.5	10.9
K6	50.60	2.93	1.75	3.7	10.4	6.5	7.6
M1	4.08	0.23	1.07	7.8	36.3	8.3	8.5
M2	1.64	0.13	0.50	9.4	21.9	4.7	4.5
M3	7.22	0.73	0.89	4.6	11.6	4.1	9.1
M4	5.90	0.53	0.59	8.1	23.5	4.8	4.0
M5	10.29	0.11	3.19	13.4	31.4	44.2	13.7
M6	1.51	0.28	0.33	8.1	16.7	2.6	3.3
M7	5.29	0.19	1.22	10.8	28.9	13.3	5.9
M8	197.36	2.93	9.29	3.5	11.0	32.3	35.4
M9	6.30	0.44	1.17	5.9	19.5	6.9	7.2
N1	28.22	4.67	0.43	6.2	14.7	2.7	3.8
N2	37.24	0.28	9.91	6.1	21.9	59.5	44.8
N3	340.63	8.42	3.23	1.2	17.1	3.9	31.2
N4	5.85	3.47	0.29	2.6	5.8	0.7	3.4
N5	14.36	0.56	1.97	5.7	14.6	11.3	14.2
O1	45.60	0.62	5.42	3.5	13.7	18.8	10.5
O2	47.38	0.27	7.86	8.5	19.2	66.5	19.2
O3	30.84	8.79	1.43	0.9	3.0	1.3	5.0
O4	12.20	1.36	3.05	1.2	3.0	3.7	7.0
O5	5.81	0.54	0.93	4.3	10.4	4.0	3.9
P1	56.70	0.24	5.16	20.1	57.9	103.6	34.8
P2	34.62	0.32	5.13	9.1	32.0	47.7	50.4
P3	21.97	0.41	3.70	6.5	20.4	24.1	31.5
P4	42.08	0.34	5.06	10.8	44.8	54.7	38.0
P5	5.77	0.23	1.40	7.8	20.1	11.0	12.7
S1	12.53	0.57	1.50	5.9	14.6	8.9	17.4
S2	8.57	0.17	1.84	11.9	39.6	21.9	14.5
S3	15.26	0.65	1.41	7.3	20.1	10.2	11.2
S4	10.36	0.12	3.16	11.1	50.3	35.2	20.9
S5	19.87	0.11	8.74	9.3	21.3	81.5	26.0
S6	74.80	1.13	1.50	18.6	36.6	27.5	7.7
S7	158.00	0.52	11.42	11.9	39.6	135.7	82.0

although the number of samples collected was four in 1979 and eight in 1980 and 1981. To extend this analysis for the 1978 data, when the P was sampled only twice (cycles 5 and 7), we regressed the mean P in the 1979–81 data for cycles 1–4 against the mean P for cycles 5–8 ($r^2 = 0.77$) and used the observed regression line to extrapolate the mean P for cycles 1–4 for each lake in 1978. The overall seasonal P for 1978 is thus based on the measured values for cycles 5 and 7 and extrapolated values for the earlier cycles. When the mean phytoplankton abundance was plotted against mean P, three of the lakes (K3, P5, and M8 in 1978) fell outside of the range of values for the remainder of the lake set. Therefore, these three 1978 lakes have been omitted in the subsequent analyses. Due to some uncertainty over the validity of our handling of P values in 1978, many of the analyses that follow have been carried out both for all 4 yr and for 1979–81.

Three of the lakes (M8, O1, and N4) show extreme variability between years both in their average phytoplankton abundance and in mean epilimnetic P (Fig. 1a), as well as variability in the composition of the remaining planktonic community. In clustering the lakes by the structure of their planktonic community, these lakes tended to be the sole members of their respective clusters, at least for 1 yr. Consequently, they were omitted from the cluster analysis and also from many of the subsequent analyses. Had they in fact been included, the within-cluster regressions (reported later) would essentially remain unaltered, since no regression analyses could be performed on single membership clusters.

The general relationship between total phytoplankton biomass and mean epilimnetic P for the now restricted data set is shown in Fig. 1b. Ideally, we would like to compare the P concentration data with primary production rather than biomass; however, no empirical data are available on primary production in our lakes. Generally speaking, there is a relationship between phytoplankton cell size and cell growth rate or maximum intrinsic rate of growth (Fenchel 1974), although the actual rate of growth also depends on nutrient availability, light, etc. (Nalewajko et al. 1981; Schlesinger et al. 1981). As a first-order approximation, we have used Fenchel's average size versus turnover rate relationship to arrive at what we call a "turnover rate corrected biomass" or TRC biomass for

TABLE 3. List and description of physicochemical and biotic variables.

Variable	Description
Geology	Percentage of drainage basin in limestone, other carbonates, conglomerates, nephaline, anorthosite, felsics, metavolcanics, quartzite
HydroLab (epilimnetic means, $N = 8$; Apr.−Sept.)	Temperature (°C), conductivity ($mS \cdot m^{-1}$), pH
	Dissolved oxygen ($mg \cdot L^{-1}$), oxidation−reduction potential (pE)
Morphometry	See Table 2
Nutrients (annual means, $N = 2$, 1978; $N = 4$, 1979; $N = 8$, 1980)	Ca, Mg, Na, K, Fe, Mn, P, SRP, Cl, Si, SO_4, NH_4, $NO_2 + NO_3$, TOC, DIC, TKN
Heavy metals	Al, Ni, Zn, Cu
Phytoplankton (annual means, $N = 8$)	Equivalent spherical diameter (μm)
P1	0.00−2.00
P2	2.00−5.00
P3	5.00−10.0
P4	10.0−30.0
P5	30.0+
P6	Filamentous
Nannoplankton	P1 + P2 + P3 + P4
Netplankton	P5 + P6
Zooplankton (annual means, $N = 8$)	Length (mm)
	Herbivores:
Z1	0.00−0.29
Z2	0.30−0.49
Z3	0.50−0.84
Z4	0.85−1.19
Z5	1.20+
	Carnivores:
Z6	0.00−0.49
Z7	0.50−0.89
Z8	0.90−1.19
Z9	1.20−1.49
Z10	1.50+

nannoplankton (i.e. the four spherical size classes less than 30 μm). Net phytoplankton biomass (filaments or sphericals greater than 30 μm) was not corrected for the turnover rate partly because we did not know how to calculate the average size of a particular filament in order to fit into Fenchel's diagram and partly because of the lesser importance of filamentous algae to higher trophic levels.

The correlations of P with nannoplankton, TRC nannoplankton, and total phytoplankton (Table 4) are generally lower than many previously reported values (e.g. Jones and Bachmann 1976; Watson and Kalff 1981). We feel that the lower values in this study likely result from a smaller range of P values in our data set and should not be taken as an indication of a weaker relationship. Jones and Bachmann's data, for example, show over a 100-fold variation in P as compared with a 10-fold variation in the LEWG data. The correlations of P with TRC nannoplankton tend to be somewhat higher than for straight biomass values. Hence, many of the subsequent analyses of nannoplankton were carried out using TRC values.

The basic correlations between mean P and mean phytoplankton biomass for nannoplankton, TRC nannoplankton, and total phytoplankton given in Table 4 are based on both arithmetic and log transformed values. The regression of the log total phytoplankton on the log P results in the following allometric equations:

$$\text{Total phytoplankton} = 12518\ P^{0.57},\ r^2 = 0.39$$

$$\text{Nannoplankton} = 5584\ P^{0.49},\ r^2 = 0.34$$

$$\text{TRC nannoplankton} = 2930\ P^{0.45},\ r^2 = 0.46.$$

The coefficients obtained in these results may be contrasted with earlier findings on the mean summer chlorophyll regressed against the mean P at spring turnover, summarized by Nicholls and Dillon (1978), with those of Oglesby (1977, Eq. 4) on chlorophyll against the P loading to summer mixed volume and with Watson and Kalff's work (1981) regressing total phytoplankton biomass against mean total P. The majority of papers quoted by the above authors report either an exponent or regression coefficient (for log−log relationships) that is greater than 1. In our studies the exponent is consistently less than 1.

Comparisons of the previous results among themselves and with the results obtained here show that while the form of the relationship generally holds, parameter values differ depending on the mix of lakes considered. Some of the reasons for this may be obvious, such as the unit criteria for the dependent variable, the variability in the fraction of the independent variable (P) that is biologically available, morphometric considerations, etc. The relationship also depends on aspects of total ecosystem structure (cf. the section

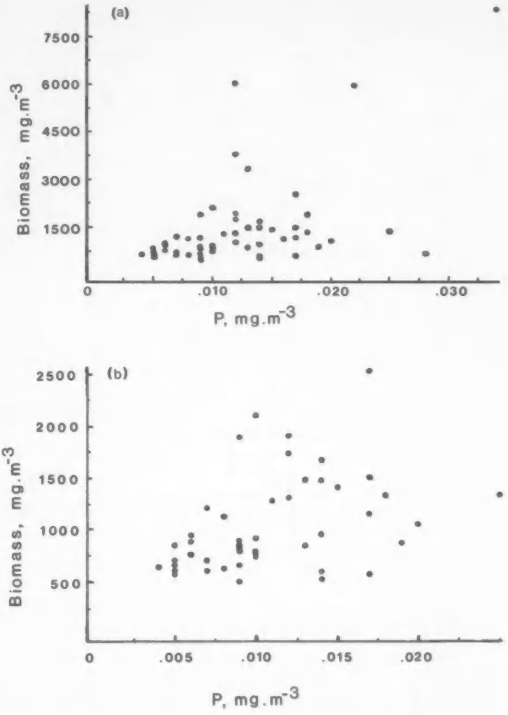

FIG. 1. Plot of the total phytoplankton biomass against the mean seasonal epilimnetic total P concentration for (a) all lakes and years and (b) restricted lake set (see text).

on cluster analyses). However, there is a fundamental difference between our results and those quoted above. When the exponent in the allometric relationship between the chlorophyll or phytoplankton biomass and P is less than 1, the chlorophyll or biomass increases at a slower rate relative to the increase in P; vice versa, when the exponent is greater than 1, the chlorophyll or biomass increases faster relative to the increase in P.

To put it differently, in phyto = P^b, when $b < 1$, we have a diminishing return to scale, and when $b > 1$, we have an increasing return to scale. We suggest that the diminishing return to scale is what one would expect when primary production, mimicked here by TRC biomass, is used as the dependent variable. Furthermore, we hypothesize that the often-observed increasing return to scale in the chlorophyll or biomass to P relationship results from a shift in the phytoplankton community from nannoplankters to larger spherical or filamentous net forms, with concomitant decreases in turnover rate as P concentration increases. With lower turnover rates, higher biomasses can be supported per given nutrient concentration; therefore, the slope of the P–biomass regression would be expected to vary as P concentration and phytoplankton community structure change. Indeed, Straskraba (1980) found slopes that moved from greater than

TABLE 4. Correlations between the mean seasonal epilimnetic P and the mean phytoplankton biomass.

	1978–81			1979–81		
		r^2			r^2	
All lakes	N	Arith.	log	N	Arith.	log
Nannoplankton	66	0.31	0.30	46	0.11	0.16
Nannoplankton[a]	66	0.37	0.42	46	0.19	0.29
Total phytoplankton	66	0.26	0.33	46	0.06	0.23
Restricted lake set[b]						
Nannoplankton	56	0.38	0.34	38	0.15	0.17
Nannoplankton[a]	56	0.48	0.46	38	0.27	0.32
Total phytoplankton	56	0.29	0.39	38	0.19	0.29

[a] Turnover rate corrected biomass value.
[b] Lakes O1, M8, and N4 deleted, as well as K2 and P5 for 1978.

to less than 1 as progressively lower concentration ranges of P were used. Similarly, the chlorophyll to primary production ratio appears to decrease with increasing levels of chlorophyll (Oglesby 1977). Hence, the small range and the relatively low P values in the present study ($P < 40\ \mu g \cdot L^{-1}$), compared with the ranges from the previously cited studies, may both be important factors in our finding of an exponent less than 1. It is also possible that factors other than P are of overriding importance in some of our lakes. However, incorporation of ambient inorganic nitrogen concentrations into the independent variable does not improve the relationships.

Role of Environmental Variables and Ecosystem Structure

Multiple Squared Correlation Analyses

The P–phytoplankton relationship may also depend on the geological composition of the drainage basin and its influence on other chemical species in the water column, as well as on the structure of the plankton community as a whole (Schindler 1978). These questions were examined by regressing the phytoplankton biomass on P and on other abiotic and biotic variables and by classifying the lakes on the basis of geology, water chemistry, and ecosystem structure.

Inclusion of the effect of grazers (herbivorous zooplankton) explains a statistically significant higher proportion of variance in phytoplankton than in the P values alone (Table 5), although the improvement is not substantial. Similarly, the inclusion of the morphological variables increases the R^2 value significantly, although, again, this improvement is not spectacular. In this latter case, however, one must bear in mind that measured epilimnetic P incorporates the effect of some morphological variables such as flushing and sedimentation rate; hence, their effect is in a way already included in a simple correlation between the phytoplankton and P.

The multiple squared correlation coefficient between the nannoplankton and P plus the HydroLab variables is somewhat higher than between the phytoplankton and P plus morphology. The improvement, however, may be somewhat suspect, since many of the HydroLab variables (especially DO, pH, and ORP) reflect either the abundance or the activity of the phytoplankton. However, the correlation between the total phytoplankton and P plus the HydroLab variables is

TABLE 5. Multiple correlations (R^2) between the phytoplankton biomass as dependent variable and the mean P, herbivorous zooplankton, morphology (mean depth, maximum depth, s.area, volume, perimeter, percent littoral zone, and flushing rate), and HydroLab (mean epilimnion temperature, conductivity, DO, pH, and ORP) as independent variables.

	N	Herbivorous zooplankton	Morphology	HydroLab
Nannoplankton[a]	56	0.61	0.58	0.71
Total phytoplankton	56	0.33	0.43	0.55

[a]Turnover rate corrected biomass.

lower than that between the total phytoplankton and P plus the morphological variables. The inclusion of morphological, HydroLab, and biotic variables increases the explained proportion of the variance in the phytoplankton, but the contribution of any of these additional variables is somewhat difficult to interpret from this type of analysis. If the relationships are ones of reciprocal cause and effect, their impact may well be different in different "types" of lakes. If this is the case, it becomes important to identify these lake types when attempting to evaluate trophic relationships. The next section details our attempt to "type" lakes using cluster analyses.

CLUSTER ANALYSES

Lakes were clustered on the basis of five different criteria and the phytoplankton to P relationship within each cluster analyzed. The five criteria were (1) the percentage of seven different rock types in the drainage basin (cf. Methods), (2) total analytical concentrations of 14 different chemicals in the water column, (3) REDEQL-II transformed free, complexed, and solid phases of each chemical element (cf. Methods), (4) total biomass densities in the four functional plankton groups, and (5) the percent densities in each of the four biomass groups.

Lakes sampled more than once during the 4-yr period were treated as different lakes; i.e. lake identification included both the lake code and the year sampled. Initially, different numbers of clusters were considered. Allowing more than seven clusters often gave us only a few lakes in most of the clusters, while fewer than seven tended to group most of the lakes together with only a few lakes in the other clusters. Qualitatively, results were the same as those in which cluster number was arbitrarily set to seven. At the time we wrote this report, the REDEQL-II transformed water chemistry was available only for 1979–80; hence, the clusterings based on the analytical and REDEQL-II transformed water chemistry as well as geology are based on data for these 2 yr only. Comparing 2 yr of data (1979–80) for biological clusters with clusters derived from 4 yr of data (not shown here) yields similar results. Therefore, we are reasonably confident in extrapolating from the geological and chemical clusterings.

Analysis of P–phytoplankton relationships within clusters is shown in Table 6. The residual sums of squares based on untransformed and log transformed values are given along with the results of the significance test (F). Somewhat surprisingly, the regressions of the phytoplankton on P are significantly different within the clusters from the overall regression for both clusterings based on the plankton community structure. No significant differences in the regressions were found between and within geology or water chemistry based clusters.

The fact that geology or water chemistry did not appear to improve the phytoplankton–P loading relationship may, of

TABLE 6. Residual sums of squares of the phytoplankton due to regression on the mean P for unclustered and clustered lakes. Lakes are clustered based on five different criteria. *, significant at 5% level; **, significant at 1% level.

	Arithmetic values			log values	
	Residual sums	df	*F*	Residual sums	*F*
Nannoplankton					
1978–81					
Unclustered	439433	54		3.0826	
Relative biomass	279092	42	2.01*	2.1609	1.49
Absolute biomass	228415	44	4.06**	1.8419	2.96**
1979–80					
Unclustered	178102	30		1.4137	
Analytical chemistry	126543	20	0.81	0.9754	0.90
REDEQL-II chemistry	87314	20	2.08	0.8957	1.16
Geology	70978	18	2.26	0.6867	1.59
Total phytoplankton					
1978–81					
Unclustered	7973356	54		6.7310	
Relative biomass	2340996	42	8.42**	2.7971	4.92**
Absolute biomass	2073526	44	12.52**	3.1581	4.98**
1979–80					
Unclustered	3583375	30		3.2998	
Analytical chemistry	2137472	20	1.35	2.0038	1.29
REDEQL-II chemistry	1905935	20	1.76	2.1977	1.00
Geology	1760301	18	1.55	1.7145	1.37

TABLE 7. Covariance analysis of the total phytoplankton biomass (tp) with P showing the effect of clustering based on the relative proportions of four functional plankton biomass groups. (*, ** as in Table 6.)

Model	Residual sums	N	F	
$tp = a_i + b_i P$	2340996	42		
$tp = a_i + bP$	3210297	49	2.17	
$tp = a + bP$	7973356	54	5.38	**
Log transformed				
$tp = a_i + b_i \log P$	2 7972	42		
$tp = a_i + b \log P$	3 7896	48	2.48	*
$tp = a + b \log P$	6 7310	54		

course, be an artifact due to our clustering procedure. Hence, different clustering procedures were also considered using a subset of the chemical and geological variables. The subset was chosen by running a stepwise regression of phytoplankton on geological or water chemistry variables and using only the four most significant geological or chemical properties for clustering. The results were still not significant.

The clusters based on relative biomass are, perhaps, the more interesting of the two clusterings that gave significantly different within-cluster regressions (Table 7). A covariance analysis based on the arithmetic values shows a common within-cluster slope but different between cluster elevations, while for transformed values even within-cluster slopes are different. The average correlation coefficient within cluster regressions is $r^2 = 0.41$ (as compared with a previous r^2 value of 0.29). If the differences in the elevation between clusters are included and the correlation coefficient is calculated from $R^2 = 1 -$ (within-cluster regression sums)/(total corrected sums), the correlation coefficient increases to $R^2 = 0.97$.

We feel the clusters represent different functional lake types (Fig. 2). The types are characterized in part by the dominant functional biomass group and in part by the relative abundance of each functional group; e.g. the herbivorous zooplankton are dominant in clusters 1, 4, and 5, with the remaining plankton groups varying in their abundance. The lakes do not necessarily stay in one cluster and often change their cluster membership from one year to the next. Out of 19 lakes sampled repeatedly for at least 3 yr, only 7 remained in the same cluster, while 12 changed their cluster membership more than once. This behavior appears to be characteristic of the planktonic communities in our lakes. Even when we clustered the lakes into only two large clusters, there were still a few lakes that "flipped" from one cluster to the other. Elsewhere (Paloheimo et al. 1983), we have concluded that this behavior suggests that pelagic plankton communities exhibit neither resilience nor resistance (Holling 1973) in the face of environmental change.

Discussion

While we have shown here that phytoplankton abundance increases with increasing total P in the water column, the relationship is rather weak, with r^2 ranging from 0.29 to 0.46. The correlation is somewhat higher for what we have called turnover rate corrected nannoplankton biomass, a transformation we suggest yields a rough approximation to nannoplankton production. The rather weak correlations for P–phytoplankton compared with previously reported literature values are, in our opinion, due to the small range in P concentration encountered in our data set and not indicative of a weaker phytoplankton–P relationship than that observed by others.

The nannoplankton–P relationship is influenced by the biomass of grazers and the lake morphology. However, given the effect of grazers, the lake morphology only marginally improved the multiple R^2 (from $R^2 = 0.61$ to $R^2 = 0.71$). Conversely, given the effect of morphology, the abundance of grazers seemed to have more of an effect on the nannoplankton (from $R^2 = 0.57$ to $R^2 = 0.71$).

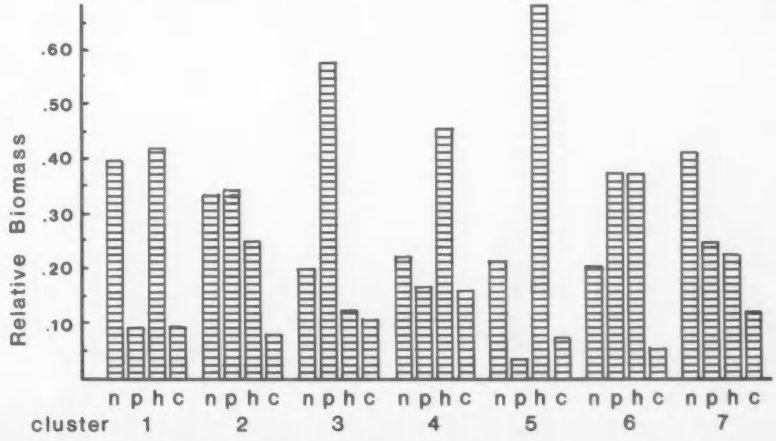

FIG. 2. Relative biomass densities ($mg \cdot m^{-3}$) in seven lake clusters. n, = nannoplankton; p, = net phytoplankton; h, = herbivorous zooplankton; c, = carnivorous zooplankton.

In all of our regressions of the phytoplankton on P, we observed a decreasing return to scale phenomena in the sense that the phytoplankton increased at a lower rate relative to the increase in concentration. This phenomenon was most noticeable with the nannoplankton and least with the total phytoplankton. This result is contrary to many of the earlier published results. We suggest that as the nutrient concentration increases, phytoplankton tend to increase in size with a concomitant decrease in their growth rate, unit metabolic cost, and nutrient requirements. Hence, at higher P concentrations, relatively higher total phytoplankton biomasses can be maintained, and an increasingly higher return to scale will be observed. The implication for the earlier studies cited here is that had the actual production values, rather than the biomass or chlorophyll values, been correlated with nutrient concentration, a decreasing return to scale would have been observed. In marine environments, where actual primary production has been measured and correlated with P concentration, an exponent less than 1 has indeed resulted across a wide range of P concentrations (Blackburn 1973).

The relationship between P and phytoplankton is also dependent on the structure of the entire planktonic community. This can be explained in part by the reciprocal interactions between water chemistry, morphology, and the plankton, and it may also be due in part to a shift from the nannoplankton to net plankton as loading increases. While the phytoplankton–total P relationship is generally valid, its specific form depends both on the mix of systems considered and the range of P concentrations observed.

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Zooplankton and Trophic State Relationships in Florida Lakes[1]

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BAYS, J. S., AND T. L. CRISMAN. 1983. Zooplankton and trophic state relationships in Florida lakes. Can. J. Fish. Aquat. Sci. 40: 1813–1819.

Zooplankton, including ciliated protozoans, were collected from 39 Florida lakes of widely ranging trophic state. Annual mean biomass values for different zooplankton groups were regressed against Carlson's Trophic State Index based on annual mean chlorophyll *a* concentration. Whereas total zooplankton biomass yielded a significant regression with increasing trophic state, microzooplankton (ciliates, rotifers, and nauplii) accounted for more of the relationship than macrozooplankton (cladocera, calanoids, and cyclopoids). Within the microzooplankton, the regression improved with decreasing body size. Macrozooplankton biomass exhibited a weak statistical relationship with lake trophic state, but the different component groups were variable in their response. The dominance within the zooplankton community shifts from macrozooplankton to microzooplankton with increasing trophic state, and the microzooplankton can constitute between 50 and 90% of the total zooplankton biomass in eutrophic lakes. Changes in zooplanktivore community structure with increasing trophic state show that whereas total fish biomass increases, dominance shifts from visually oriented predators, such as bass and bluegill, to pump filter-feeding planktivores, such as gizzard shad (*Dorosoma cepedianum*). While Florida zooplankton communities are similar in size structure to tropical communities, no statistically significant differences were found between empirical equations of crustacean zooplankton biomass and trophic state determined from temperate and Florida data bases.

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On a prélevé du zooplancton, y compris protozoaires ciliés, de 39 lacs de la Floride couvrant un large éventail d'états trophiques. On a calculé les régressions des valeurs de biomasse moyenne annuelle pour différents groupes de zooplanctontes contre l'indice de l'état trophique de Carlson fondé sur la chlorophylle *a* moyenne annuelle. Alors qu'il y a régression significative entre la biomasse zooplanctonique totale et un état trophique en voie d'amélioration, le microzooplancton (ciliés, rotifères et nauplii) est davantage responsable de la relation que le macrozooplancton (cladocères, calanoïdes et cyclopoïdes). Parmi le microzooplancton, la régression s'améliore à mesure que diminue la taille corporelle. La biomasse macrozooplanctonique montre une faible relation statistique avec l'état trophique des lacs, mais la réponse des différents groupes qui la constituent est variable. La dominance au sein de la communauté zooplanctonique passe du macro- au microzooplancton à mesure qu'augmente l'état trophique, et de 50 à 90 % de la biomasse zooplanctonique totale des lacs eutrophes peut être composée de microzooplancton. Les changements dans la structure de la communauté des zooplanctivores à mesure que s'améliore l'état trophique démontrent que, tandis que la biomasse totale des poissons augmente, la dominance passe des prédateurs chassant à vue, tels que les achigans, à des planctivores filtreurs, tels que l'alose à gésier (*Dorosoma cepedianum*). Bien que les communautés zooplanctoniques de la Floride soient semblables aux communautés tropicales quant à la structure par taille, nous n'avons observé aucune différence significative entre des équations empiriques de biomasse de crustacés zooplanctoniques et l'état trophique déterminé à partir de données de régions tempérées et de la Floride.

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NUMEROUS investigations have documented changes in the size-structure, species composition, and biomass of temperate limnetic zooplankton communities with eutrophication. Total zooplankton biomass generally increases with increasing trophic state and is accompanied both by species and group replacements within the cladocera and copepods, the macrozooplankton (Brooks 1969; Hall et al. 1970; O'Brien and deNoyelles 1974), and an increased importance of microzooplankton, including the rotifers, copepod nauplii, and ciliated protozoans (Gannon and Stemberger 1978; Pace and Orcutt 1981). Within the macrozooplankton, cyclopoid copepods and cladocerans assume greater importance relative to calanoid copepods (Gliwicz 1969; McNaught 1975), and large-bodied cladocerans (*Eubosmina coregoni* and large *Daphnia*) are replaced by smaller bodied taxa (*Bosmina longirostris* and small *Daphnia*) in eutrophic lakes (Brooks 1969).

The relationships between such changes and eutrophication have been considered to be indirect and mediated through changes in quality and intensity of predation (Brooks 1969). Planktivorous fish increase in importance with trophic state (Larkin and Northcote 1969), and as the intensity of size-selective predation increases, the susceptibility of larger zooplankton to such predation increases (Zaret 1980). In addition, invertebrate predators (i.e. *Chaoborus*, copepods, and cladocera) may significantly alter the abundance and size–structure of the zooplankton community (McQueen 1969; Federenko 1975). The impact of cyclopoid predation in eutrophic lakes has been demonstrated to be more important than fish predation (Gliwicz et al. 1978; Lane 1979).

Inter- and intra-specific competition between different sized herbivores over available particle size spectra may alter the size–structure of zooplankton communities (Hall et al. 1976). Inhibition of filtering rates through mechanical interference associated with filamentous and colonial blue-green algae, as well as chemical antagonism through toxic algal metabolic production (Porter 1977), can also decrease the abundance of zooplankton, particularly cladocerans, in eutrophic lakes.

With a few exceptions (Patalas 1972; Sprules 1975; Pederson et al. 1976), most studies of zooplankton changes with trophic state in temperate lakes have not been based on detailed interlake comparisons within a given geographical region. Only a few studies in temperate lakes have considered changes in the relative importance of microzooplankton and macrozooplankton with increasing trophic state (Gannon and Stemberger 1978; Ejsmont-Karabin et al. 1980), and investigations into ciliated protozoans are almost totally lacking.

This study was designed to determine statistical relationships between zooplankton communities and trophic state in subtropical Florida lakes and to compare these with similar relationships found in temperate lakes. The anticipated role of the ciliated protozoans in the microzooplankton is considered, and preliminary assessments of planktivore community structure are made.

Methods

Limnetic zooplankton communities were analyzed from 39 lakes throughout peninsular Florida representing a gradient of trophic state conditions (1–120 mg/m^3 annual mean chlorophyll *a*). Lake depths ranged from 1 to 20 m, and with the exception of nine lakes, all had mean color values less than 80 chlorplatinate units. Crustacean zooplankton, rotifers, and ciliated protozoan abundances were determined from samples taken monthly during 1979 from 20 lakes (Beaver and Crisman 1982) and quarterly during 1978–79 from 15 lakes (Schulze 1980; Beaver and Crisman 1981). Monthly rotifer and crustacean zooplankton data for 1979 from four hypereutrophic lakes (Brezonik et al. 1981) have also been included.

Ciliated protozoans were collected and preserved according to the methods of Beaver and Crisman (1982), and the remainder of the zooplankton community was collected by one or two vertical hauls of an 80-μm mesh Wisconsin plankton net at a midlake station. The latter samples were preserved with buffered formalin and identified with the keys of Deevey and Deevey (1971), Edmondson (1959), and Stemberger (1979). The sampling design was determined by logistical needs and by statistical analysis on a previous intensive sampling effort for six Florida lakes sampled biweekly and monthly for 5 yr. No significant heterogeneity was indicated in zooplankton species, composition, or abundance between stations (T. L. Crisman, unpublished data).

Chlorophyll *a* concentration, uncorrected for phaeophytin, was used as the measure of lake trophic state. Composite water column samples were taken concurrently with the zooplankton samples, and concentrations were determined by the trichromatic method (American Public Health Association 1975). Annual mean values were incorporated into Carlson's (1977) trophic state index (TSICHL). Although determined from a temperate zone data base, Carlson's index has been shown to be significantly related to recent Florida-based multivariate trophic state indices, which were unavailable at the time of this analysis (Huber et al. 1982).

Annual mean biomass of ciliated protozoans for 30 of the lakes is from Beaver and Crisman (1982) and that of the remaining 9 lakes has been predicted using the biomass values and highly significant regression equations of Beaver (1980). Biomass of the remaining zooplankton components was calculated by converting abundance to micrograms C per litre using conversion factors published for individual taxa (Dumont et al. 1975; Maslin 1969). Annual mean biomass values were log transformed ($\ln (x + 1)$) in order to normalize their variance for the regression analyses.

The SAS package (Helwig and Council 1979) was used for all statistical analyses. Computing facilities were provided by the Northeast Regional Data Center, Gainesville, FL.

Results

The log transformed data for annual mean biomass values for both total zooplankton and individual zooplankton groups were regressed against the trophic state index. The positive and statistically significant relationship between total zooplankton biomass and increasing trophic state ($r^2 = 0.66$) is similar to that reported for temperate lakes (Brooks 1969; Hall et al. 1970; O'Brien and deNoyelles 1974) but unlike the latter studies includes the contribution of ciliated protozoans to total zooplankton biomass.

Total zooplankton biomass was divided into microzooplankton (ciliated protozoans, rotifers, nauplii) and macro-

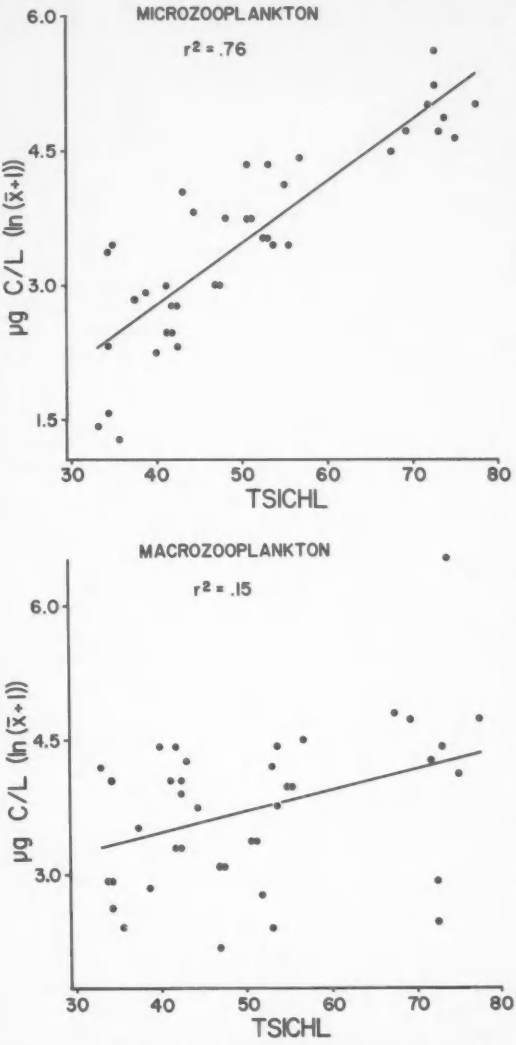

FIG. 1. Regression plots of microzooplankton and macrozooplankton biomass versus Carlson's trophic state index (TSICHL).

zooplankton (cladocerans, copepodites, adult copepods) and regressed against trophic state (Fig. 1). Microzooplankton biomass was positively related to trophic state ($r^2 = 0.76$, $P < 0.0001$), while macrozooplankton displayed a weak ($r^2 = 0.15$) but significant ($P < 0.0001$) positive relationship. The percent of total zooplankton biomass contributed by microzooplankton was significantly related to trophic state ($r^2 = 0.29$, $P < 0.0004$) and ranged from approximately 5–50% in oligotrophic lakes to 50–90% in eutrophic lakes. Thus, it appears that the positive regression between total zooplankton biomass and trophic state is determined more by changes in the importance of microzooplankton than macrozooplankton.

TABLE 1. Model parameters for regressions of log transformed mean annual zooplankton biomass (ln $(x + 1)$) and percent biomass composition as the dependent variables and Carlson's trophic state index (TSICHL) based on mean annual chlorophyll *a* as the independent variable.

Dependent variable (Y)	Slope	Intercept	r^2	$P<$
Total	0.048	2.003	0.66	0.0001
Microzooplankton	0.069	0.0035	0.76	0.0001
Macrozooplankton	0.024	2.512	0.15	0.0159
Ciliata	0.069	−0.505	0.77	0.0001
Rotifera	0.0605	−1.002	0.54	0.0001
Nauplii	0.044	−0.526	0.33	0.0001
Cyclopoida	0.034	0.618	0.34	0.0001
Cladocera	0.043	0.053	0.23	0.0001
Calanoida	0.043	1.929	0.07	0.1024
Microzooplankton as % of total	0.898	−0.879	0.29	0.0004

The biomass of individual zooplankton components comprising the microzooplankton yielded significant regressions with lake trophic state (Table 1). The best statistical relationship was displayed by the ciliates ($r^2 = 0.77$), followed by rotifers ($r^2 = 0.54$) and nauplii ($r^2 = 0.33$). Thus, while microzooplankton biomass as a whole displays a better relationship with trophic state than macrozooplankton, the regression of individual microzooplankton components decreased with a general increase in body size.

Within the macrozooplankton, cladoceran biomass yielded a weak but significant ($r^2 = 0.23$, $P < 0.0001$) positive regression with lake trophic state. Cyclopoid copepod biomass also yielded a significant positive regression ($P < 0.0001$), and more of the variance ($r^2 = 0.34$) was accounted for by trophic state than in the cladoceran regression. However, the linear regression of calanoid biomass with trophic state was the weakest of any macrozooplankton component ($r^2 = 0.07$) (Table 1).

The distribution of calanoid biomass along our trophic gradient is actually better described by a U-shaped curvilinear relationshp ($r^2 = 0.24$, $P < 0.0066$), which may in part be a reflection of a change in the dominant *Diaptomus* species in eutrophic lakes (Fig. 2). Three *Diaptomus* species (*D. floridanus*, *D. mississippiensis*, *D. dorsalis*) were present in oligotrophic–mesotrophic lakes, with the former two species being dominant, and total calanoid biomass declined slightly with increasing trophic state. Conversely, biomass in eutrophic lakes was generally greater than in mesotrophic lakes, and *D. dorsalis* usually was the only calanoid species present.

As a means of assessing potential vertebrate predation upon the macrozooplankton, we regressed total fish biomass data and the percent contribution of fish biomass by sport, rough, and forage fishes against Carlson's trophic state index. The fish data were obtained from summary reports of blocknet samples of 30 Florida lakes (10 of which were included in our study) by the Florida Game and Fresh Water Fish Commission. The composition of fish groups was taken from Kautz (1980).

The total biomass of fish generally increases with eutrophication in Florida lakes and is accompanied by changes

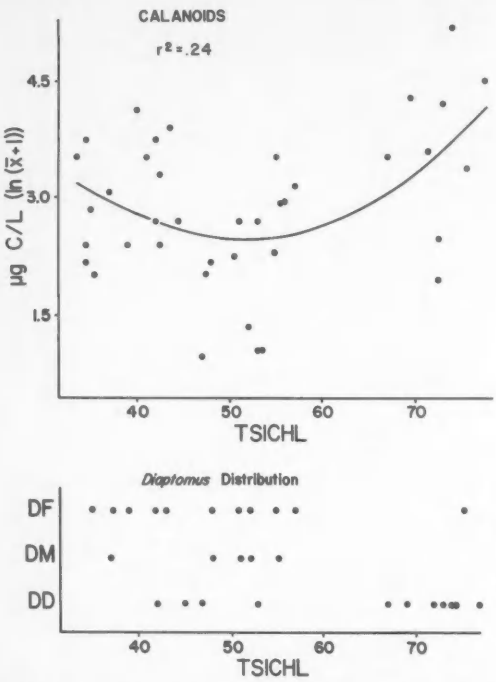

FIG. 2. Diaptomid species composition and regression plot of calanoid biomass versus Carlson's trophic state index (TSICHL). Model is $Y = 9.15 - 0.262(\text{TSICHL}) = 0.026(\text{TSICHL})^2$, $r^2 = 0.24$, $P < 0.0066$. DF, *Diaptomus floridanus*; DM, *Diaptomus mississippiensis*; DD, *Diaptomus dorsalis*. Closed circle indicates presence of species.

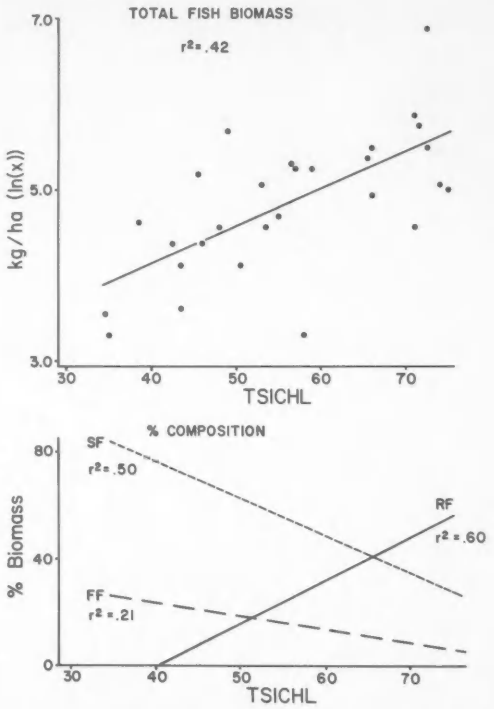

FIG. 3. Regression plot of total fish biomass (log (kg/ha), upper panel) and predicted percent composition of various fish groups (lower panel) versus Carlson's trophic state index (TSICHL). SF, sport fish; FF, forage fish; RF, rough fish. See text for details.

in species composition (Fig. 3; Table 2). On a percentage basis, oligotrophic lakes are dominated by sport fish (principally Centrarchidae) and forage fish (Cyprinidae, Cyprinodontidae, Atherinidae, Poeciliidae). Dominance in eutrophic lakes shifts to rough fish, especially gizzard shad (*Dorosoma cepedianum*), a species often exceeding 80% of total fish biomass. These results are similar to those found in temperate lakes, with planktivorous fish increasing in abundance and community dominance with eutrophication.

Discussion

Subtropical lakes differ from temperate lakes in a number of respects. Most Florida lakes are shallow and circulate continuously. The growing season is greatly extended and mesotrophic and eutrophic lakes are generally dominated year round by blue-green algae (Brezonik et al. 1981). Within the macrozooplankton, large *Daphnia* are absent, and the abundance of cladocerans generally is reduced during summer.

While total zooplankton biomass displayed a positive regression with increasing trophic state in Florida lakes, it is clear that this relationship is controlled more by the microzooplankton than by the macrozooplankton component. Even within the microzooplankton, the regression improved with decreasing body size, with ciliated protozoans displaying the best relationship of any zooplankton component. In addition, detailed analysis of ciliates from our lakes (Beaver and Crisman 1982) indicated that large-bodied (>30 μm) taxa dominate the assemblages of oligotrophic lakes, while eutrophic lakes are dominated by small-bodied (<30 μm) taxa. Although comparable data for ciliates and nauplii are lacking for temperate lakes, the relationship between rotifer biomass and the trophic state of Florida lakes agrees with that of temperate systems (Hakkari 1972; Gannon and Stemberger 1978).

Microzooplankton are likely to be more susceptible to invertebrate predation than are macrozooplankton (Zaret 1980). Cyclopoid copepods often feed on rotifers (McQueen 1969) and nauplii (Confer and Blades 1975) and can significantly reduce their abundance (Confer 1971; Lane 1979). Although cladocerans (Porter et al. 1979), copepods (Berk et al. 1977), and the rotifer *Asplanchna* (Maly 1975) prey on ciliated protozoans, it has not been shown that they are the prime factor controlling either the abundance or community structure of ciliates in lakes.

The abundance of *Chaoborus* larvae was always extremely low in our Florida lakes, but it is likely that their populations were greatly underestimated by the sampling technique employed. *Leptodora*, a predaceous cladoceran, was found in

TABLE 2. Model parameters for regression models of total fish biomass and percent composition of sport, rough, and forage fish against lake trophic state (TSICHL).

Dependent variable	Slope	Intercept	r^2	$P<$
log total fish biomass	0.0425	2.452	0.42	0.0002
% sport fish	−1.374	131.307	0.50	0.0001
% rough fish	1.593	−64.199	0.60	0.0001
% forage fish	−0.540	45.582	0.21	0.0120

only one sample, and the biomass of cyclopoid copepods displayed a weak regression with increasing trophic state. Although our data do not indicate a change in the intensity of invertebrate predation with increasing trophic state, it is suggested that if invertebrate predation is important in structuring microzooplankton community structure it is least pronounced for ciliates and rotifers whose rapid turnover times (Allan 1976) may greatly exceed cyclopoid and *Chaoborus* predation rates and turnover times.

Small-bodied ciliates (<30 μm) are principally bactivorous, feeding on particles as small as 0.2 μm, with maximum efficiency between 0.3 and 1.0 μm (Fenchel 1980), but large-bodied ciliates are predominantly phytophagous (Fenchel 1980; Goulder 1972) and generally ineffective at grazing bacteria-sized particles (<1.0 μm). Bacterial grazing also has been documented for nauplii (Gophen et al. 1974; Monakov and Sorokin 1972) and rotifers (Haney 1973; Starkweather et al. 1979), although the importance of bacteria in the diet of the latter depends on the concentration of associated algae and the presence of a ciliated buccal funnel and a malleate mastax (Bogdan et al. 1980).

It appears that the smaller the body size of zooplankton, the greater the dependence on bacteria as a food source. Since maintenance of bactivorous ciliate populations requires bacteria concentrations in excess of 10^6/mL and since such concentrations are rarely found in oligotrophic lakes (Porter et al. 1979), it is not surprising that the abundance of microzooplankton in general and ciliates in particular displays a strong positive relationship with increasing trophic state.

Within the macrozooplankton, cladoceran and cyclopoid biomass displayed a weak linear regression with increasing trophic state, while that of calanoids was curvilinear. The cladoceran trend is similar to that observed in temperate lakes (Hall et al. 1970; O'Brien and deNoyelles 1974; McNaught 1975), but regardless of trophic state, cladoceran assemblages in Florida lakes consist of only small daphnids and bosminids (principally *Daphnia ambigua* and *Eubosmina tubicen*), whereas temperate lakes are characterized by greater species richness and larger body size.

The weak curvilinear relationship of calanoid biomass with increasing trophic state may reflect the shift in species composition from predominately *Diaptomus floridanus* and *D. mississippiensis* in oligotrophic and mesotrophic lakes to *D. dorsalis* usually being the sole calanoid in eutrophic lakes. Although all three species may be present, Elmore (1980) presented evidence that the smaller two species (*D. floridanus*, *D. mississippiensis*) are able to outcompete the larger *D. dorsalis* in oligotrophic and mesotrophic Florida lakes, whereas the dominance of the latter species in eutrophic lakes is a reflection of its decreased susceptibility to vertebrate predation.

Werner et al. (1978) compared fish community structure of oligotrophic Florida and Michigan lakes and found that they were similar, with a majority of the biomass in both regions being contributed by bluegill (*Lepomis macrochirus*) and bass. Thus, predation intensity on macrozooplankton appears to be comparable in temperate and subtropical oligotrophic lakes.

Major differences do exist in the structure and functioning of fish communities in eutrophic lakes of the two climatic zones. Although fish biomass in both zones increases with increasing trophic state, size-selective predation is intensified in eutrophic temperate lakes as a result of percid dominance (Larkin and Northcote 1969) but is reduced in comparable subtropical lakes associated with the dominance (>80% of total fish biomass) of pump filter-feeding gizzard shad. The diet of the gizzard shad is more varied than that of percids and is composed of algae and detritus in addition to zooplankton. Drenner et al. (1982) demonstrated that predation by shad on zooplankton is attributed more to pump filter-feeding than to sight selective predation. In a series of field experiments they showed that shad predation decreased the abundance of rotifers, cladocerans, copepod nauplii, *Chaoborus*, and cyclopoid copepodids and adults but had no impact on that of copepodid or adult *Diaptomus pallidus*. Thus, based on the work of Elmore (1980) and Drenner et al. (1982) the somewhat curvilinear relationship of *Diaptomus* biomass, the largest bodied Florida zooplankter, with increasing trophic state may be explained by a shift in species composition to *D. dorsalis* with eutrophication, a species capable of evading shad predation.

The importance of changes in the intensity of vertebrate predation on the structure of macrozooplankton communities with increasing trophic state is more difficult to evaluate for Florida than for comparable temperate lakes. This is attributed to the fact that Florida lakes, regardless of trophic state, are characterized by reduced species diversity, the absence of large-bodied species, which are affected most noticeably by changes in vertebrate predation, and the dominance of pump filter-feeding shad rather than sight-selective predators in eutrophic lakes. While shad can potentially greatly reduce macrozooplankton biomass in eutrophic lakes, this may not be accompanied by either a body size or species shift.

As a means of assessing the importance of food resources as a factor in the structuring of macrozooplankton communities, McCauley and Kalff (1981), through a series of regression equations, related total crustacean biomass in temperate lakes to changes in phytoplankton availability with increasing trophic state. Regression of total crustacean biomass against chlorophyll *a* yielded a significant positive linear relationship ($r^2 = 0.72, P < 0.001$). An identical analysis of our Florida data gave a similar relationship ($r^2 = 0.41$; $P < 0.0001$), which was not significantly different ($P < 0.01$) between slopes and intercepts.

McCauley and Kalff (1981) also plotted the ratio of crustacean biomass to chlorophyll *a* against chlorophyll *a* as an approximate measure of the efficiency of zooplankton production and obtained a decreasing asymptotic relationship with increasing trophic state. Using the regression equation of Watson and Kalff (1981) to estimate the contribution of

nannoplankton to total phytoplankton biomass in their lakes, they then regressed the ratio of crustacean biomass to nannoplankton biomass against chlorophyll *a* and showed that the ratio is constant over a trophic state gradient.

In spite of the general increase of total phytoplankton biomass with increasing trophic state, the ratio of net plankton to nannoplankton biomass increases (Watson and Kalff 1981). Given that crustacean biomass displayed a declining asymptotic relationship with increasing trophic state while appearing to track the availability of nannoplankton closely, coupled with the fact that much of the net plankton fraction appears to be unavailable for macrozooplankton utilization (Porter 1977), McCauley and Kalff (1981) concluded that the lack of a strong positive relationship of crustacean biomass to increasing trophic state may be a reflection of the decreased availability of nannoplanktonic food resources.

Although we lack phytoplankton data for our lakes and estimates of the proportion of total chlorophyll *a* contributed by nannoplankton based on regression equations for temperate lakes may not be applicable to the subtropics, a plot of the ratio of crustacean biomass to chlorophyll *a* against chlorophyll *a* produced the same declining asymptotic relationship to increasing trophic state described by McCauley and Kalff (1981) for temperate lakes. The stronger regression of nauplii and adult cyclopoids to increasing trophic state in Florida relative to that of calanoids and cladocerans suggests that the relationship of crustacean biomass to chlorophyll is more complicated than envisioned by McCauley and Kalff and may be complicated by the effects of differential vertebrate predation.

Although similar quantitative data on the regional relationship of tropical zooplankton to trophic state do not exist, qualitative comparisons between climatic zones can be made. Burgis (1974) noted that the crustacean zooplankton production of Lake George, Uganda, is not much higher than that of comparable temperate lakes. Fernando (1980) showed that tropical zooplankton communities display a definite reduction in species diversity and body size. Limnetic copepods are typically dominated by one or two species of small (maximum length of 1.8 mm) cyclopoids or calanoids (Burgis and Walker 1971; Fernando 1980). Tropical cladocerans are generally smaller bodied than temperate assemblages (Fernando 1980) and usually are dominated by one species of *Daphnia* (Burgis and Walker 1971; Fernando 1980) and a combination of bosminids, moinids, *Ceriodaphnia*, and *Diaphanosoma*. The size-structure of Florida communities is similar.

The causal mechanism for a reduction in body size in the subtropics and tropics is not clear. Fernando (1980) concluded that constantly high water temperatures would decrease the fitness of large cladocerans, thus favoring better adapted small-bodied taxa. In Florida, where only small-bodied cladocerans occur, sexual reproduction in *Daphnia* occurs mainly in late spring and early summer with the near elimination of adults during the hottest months of summer (J. S. Bays and T. L. Crisman, unpublished data). Connell (1975) suggested that abiotic factors were important only from the perspective of their influence on environmental stability and hypothesized that increased vertebrate predation in the tropics was responsible for the dominance of small taxa in macrozooplankton.

Florida zooplankton communities appear to be more similar in size-structure to tropical rather than temperate assemblages, but their relationship to lake trophic state is not statistically different from that found in temperate lakes. Microzooplankton density is probably controlled by food availability, especially bacteria. Macrozooplankton show a similar relationship to algal abundance as that found in temperate lakes, but while it is likely that the importance of fish predation in structuring zooplankton communities is similar in oligotrophic and mesotrophic lakes of the temperate and subtropical zones, differences exist between zones for eutrophic lakes due to the dominance of pump filter-feeding rather than sight-selective planktivores in Florida lakes.

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Influence of Predatory Fish Density on Trapability of Crayfish in Ontario Lakes[1]

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In 19 central Ontario lakes the catches of crayfish in baited minnow traps usually were well predicted by numbers of crayfish counted in timed underwater searches. Exceptions were lakes with relatively high predator densities, where trap catches were far less than expected from search counts. In a stepwise linear regression, an index of the density of rock bass (*Ambloplites rupestris*) in the lakes was significantly negatively correlated with trapability. Smallmouth and largemouth bass (*Micropterus dolomieui* and *M. salmoides*), despite their reputation for consuming crayfish, were not significantly correlated with variations in trapability across lakes, but they reduced trapability and altered crayfish behavior in one lake. Yellow perch (*Perca flavescens*) density was positively correlated with trapability. The predatory basses appear to reduce trapability of crayfish more than they affect crayfish density; high crayfish populations were found in some lakes with dense bass populations. Predator-mediated changes in trapability seem consistent across the crayfish species *Orconectes propinquus*, *O. virilis*, and *Cambarus robustus*. In aquaria without predators, *O. propinquus* from a lake with high bass density were more nocturnal, more shelter-bound, and less active than those from a lake without bass. Behavior of females differed more between these two lakes than that of males, which are less vulnerable to predation than females. These behavior differences persisted for at least 3 wk in the laboratory, indicating that interspecific comparisons of behavior could be misleading unless the populations studied had similar histories of predation risk. The observed interlake variation in trapability suggests that catches in passive traps may be poor indices of crayfish density.

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Dans 19 lacs du centre de l'Ontario, on peut assez bien prédire les prises d'écrevisses dans des pièges à ménés appâtés sur la base des nombres observés au cours d'explorations subaquatiques chronométrées. Il y a toutefois exceptions dans le cas de lacs à densités de prédateurs relativement élevées, dans lesquels les prises des pièges sont de beaucoup inférieures à celles anticipées à la suite des recensements sous l'eau. Dans une régression linéaire en gradins, on observe une corrélation négative entre un indice de densité des crapets de roche (*Ambloplites rupestris*) dans les lacs et le potentiel de piégeage. Bien que les achigans à petite et à grande bouche (*Micropterus dolomieui* et *M. salmoides*) aient la réputation de consommer des écrevisses, il n'y a pas de corrélation significative entre ces espèces et les variations de potentiel de piégeage d'un lac à l'autre, mais ces achigans diminuent le potentiel de piégeage et modifient le comportement des écrevisses dans un lac. Il y a corrélation positive entre la densité des perchaudes (*Perca flavescens*) et le potentiel de piégeage. Les achigans prédateurs semblent réduire la capturabilité des écrevisses plus qu'ils n'influencent la densité de ces dernières; on observe d'abondantes populations d'écrevisses dans certains lacs à fortes densités d'achigans. Les changements de potentiel de piégeage dus aux prédateurs semblent uniformes chez les trois espèces d'écrevisses *Orconectes propinquus*, *O. virilis* et *Cambarus robustus*. Dans des aquariums dépourvus de prédateurs, *O. propinquus* provenant d'un lac à fortes densités d'achigans est plus nocturne, cherche davantage les abris et est moins actif que

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les sujets provenant d'un lac dépourvu d'achigans. Le comportement des femelles diffère dans ces deux lacs de façon plus prononcée que celui des mâles, moins vulnérables à la prédation que les femelles. Ces différences de comportement persistent en laboratoire pendant au moins 3 semaines, ce qui indique que des comparaisons interspécifiques de comportement peuvent induire en erreur, à moins que les populations étudiées n'aient présenté dans le passé le même risque de prédation. La variation de potentiel de piégeage d'un lac à l'autre donne à penser que les prises de pièges passifs sont de mauvais indices de densité des écrevisses.

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WHILE analyzing data from a benthic survey of a diverse group of Ontario lakes, we noticed that crayfish catches in baited minnow traps were always very low in lakes having relatively high densities of predators on crayfish, specifically largemouth, smallmouth, and rock bass (*Micropterus salmoides*, *M. dolomieui*, and *Ambloplites rupestris*). Lakes with low densities of these fishes yielded a wide range of trap catches. Underwater observations indicated that the low trap catches in lakes with high predator densities were not simply the result of depleted crayfish populations. In one lake with high bass densities, divers repeatedly found abundant crayfish in places where traps had yielded nothing; they estimated that crayfish were more abundant there than in all but 2 of the 14 lakes surveyed. It appeared, therefore, that predators might be influencing the behavior of crayfish in ways that reduced their susceptibility to passive gear such as traps. Such behavioral alterations could seriously limit the utility of trap catches as indices of crayfish density across sites differing in predator density.

Effects of a predatory fish on behavior of one crayfish species are already well documented. Stein and Magnuson (1976) and Stein (1977) showed that *Orconectes propinquus* reduced time spent active and restricted its substrate preferences to areas with cover when smallmouth bass were present with them in laboratory aquaria. They also showed that the susceptibility of *O. propinquus* to smallmouth bass predation varied with crayfish size, sex, and reproductive condition and that behavioral responses to the presence of predators were usually most marked in the most susceptible stages. Similar behavioral modifications might be occurring in the four crayfish species in our lakes, leading to marked differences in trapability between lakes with high and low bass densities.

Of course, predators might be affecting crayfish population density as well. Of the fish species common in our lakes, yellow perch (*Perca flavescens*), rock bass, largemouth bass, smallmouth bass, and brown bullhead (*Ictalurus nebulosus*) all feed substantially on crayfish (Fedoruk 1966; Keast and Webb 1966; Keast and Welsh 1968; Laarman and Schneider 1972; Scott and Crossman 1973; Clady 1974; Stein and Magnuson 1976; Keast 1977; Stein 1977). Stein and Magnuson (1976) suggested that where fish predators are abundant they could account for 25% of total crayfish mortality.

This article reports results of a second crayfish trapping survey specifically designed to evaluate the influence of trapability changes on trap catches. In addition, we demonstrate behavioral differences between *O. propinquus* from lakes with high and low bass densities that persist in the absence of predators and which probably account for some of the observed trapability differences.

Methods

THE LAKES

Nineteen central Ontario lakes spanning a wide range of physical, chemical, and biotic characteristics were surveyed in 1978–81 by the Lake Ecosystem Working Group at the University of Toronto. Detailed information on the limnology and biota of the lakes can be found in Collins et al. (1981), Gates et al. (1983), Paloheimo and Zimmerman (1983), Sprules and Knoechel (1983), and Sprules et al. (1983). The lake identification codes used in this article are consistent with those in the abovementioned studies.

Four species were the major crayfish in at least one lake: *O. propinquus*, *O. virilis*, *O. obscurus*, and *Cambarus robustus*. In all but one lake our trap catches were almost monospecific, with subordinate species accounting for less than 10% of the catch.

CRAYFISH ABUNDANCE MEASURES

About 30 standard Gee's hardware cloth minnow traps (30 cm diameter × 60 cm long), with entrances enlarged to 5 cm in diameter were baited with 50 g of beef (or, rarely, pork) liver and set in less than 3 m of water at approximately even intervals around the entire perimeter of each lake. Traps were usually placed in areas of cover, such as wood debris, rocks, or macrophytes. When such cover was absent traps were placed on sand. Traps were set in the late afternoon or early evening during July 1980 and recovered before 13:00 the following day, and the catches were recorded and retained. All crayfish were identified (Crocker and Barr 1968), measured, and released. In the analyses, the arithmetic average catch per trap was $\log_{10}(X + 1)$ transformed to remove a correlation between mean and variance among lakes.

To determine whether time of trap recovery could influence the catch, a group of 30 traps was set in a lake near one of the surveyed lakes and the contents were counted once at dawn (06:00) and again 4 h later. Twenty-two traps contained crayfish at dawn. By 10:00, six traps had recruited another crayfish and three had lost one, modifying the average catch by less than 3%. Therefore, differences between lakes in the hour the traps were picked up probably did not significantly affect the relative catches in the lakes.

Conservative measures of the reliability of between-lake differences in crayfish trap counts are the Pearson and Spearman correlation coefficients for trapping results in the

nine lakes sampled in both 1979 and 1980. The two values are 0.94 and 0.87, respectively, indicating that the relative catches in the lakes are very repeatable.

To assess changes in trapability of crayfish between lakes, we needed an independent estimate of crayfish abundance to compare with trap counts. We used the arithmetic average number of crayfish counted during 3-min searches by divers in five locations roughly uniformly distributed along the shoreline of each lake. These searches were carried out simultaneously with the trapping survey. Before each search began the diver swam along the bottom through the epilimnetic stratum turning over debris in search of crayfish. The search therefore began with prior knowledge of the depth distribution of crayfish in each location, and divers attempted to concentrate on the most productive depth zone. This technique tended to reduce the possibility of divers improving their search efficiency as they moved through the five sites in each lake. The resulting counts are probably not completely independent of differences in crayfish behavior between lakes, but they are certainly much less dependent on such factors than are passive trap catches.

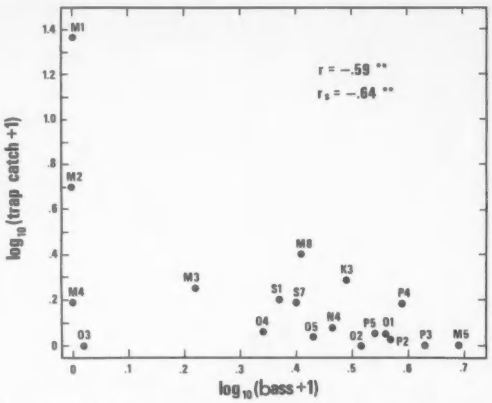


FIG. 1. Relation between average crayfish catch per minnow trap and the sum of smallmouth bass, largemouth bass, and rock bass abundance indices in 19 lakes during July 1980. Lake identifiers next to each point are consistent with those in other studies on these lakes (see Methods).

FISH ABUNDANCE MEASURES

Four types of gear were employed: variable mesh gill nets, trap nets, clear Plexiglass traps (Casselman and Harvey 1973), and large (54 cm diameter × 90 cm long) minnow traps made of black fiberglass window screening (Kushneriuk 1982) and baited with dry dogfood. Gear was set for 24 h, except for the minnow traps and Plexiglass traps, which were set overnight. Median and range (in parentheses) of total effort per lake for the four gear types were 244 m (122−914) of gill net, 4 (2−8) trap net sets, 8 (4−17) Plexiglass trap sets, and 30 (15−47) trap nights for minnow traps.

To obtain an index of fish abundance that was relatively free of bias caused by gear-specific differences in catchability of particular fish species, the following calculations were made for each of the five fish species of interest in each lake. First, the catch per unit effort (CPE) for each gear type was standardized to a 0−1 range by dividing by the maximum CPE for that gear and that species over all lakes. Then, the standardized CPE's of all types of gear were summed. Multispecific abundance indices were produced by addition of the individual species' abundance indices. All resulting fish abundance figures were $\log_{10}(X + 1)$ transformed for the analyses.

The resulting abundance indices for rock bass, brown bullhead, yellow perch, and smallmouth bass were very highly correlated with catch per square metre for these species in nighttime electrofishing surveys conducted in the littoral zone of eight of the lakes (B. Shuter and J. Casselman, Ontario Ministry of Natural Resources, Maple, Ont., personal communication). Pearson correlation coefficients for the above species were 0.99, 0.89, 0.93, and 0.97, respectively.

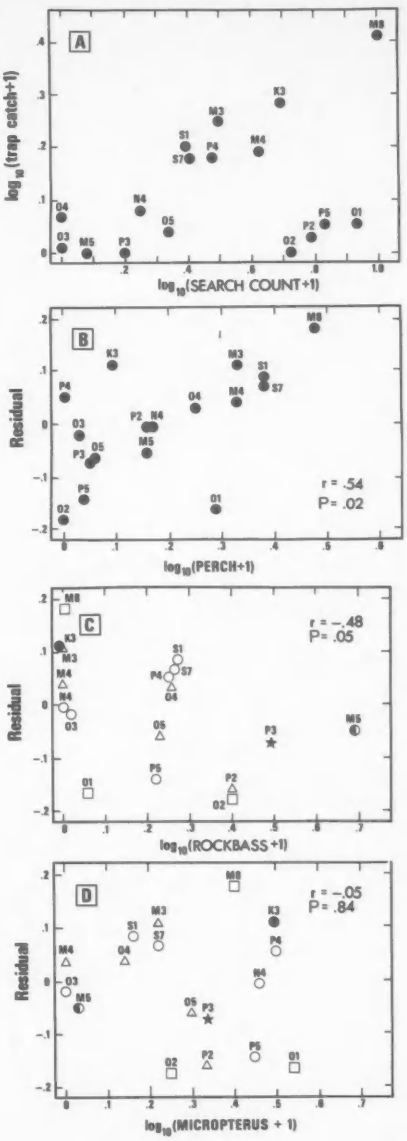
CRAYFISH BEHAVIOR

Stein and Magnuson (1976) studied differences in behavior of *O. propinquus* from a single lake with smallmouth bass present or absent from their aquaria. However, we were interested in whether crayfish from different lakes differed in their behavior in the absence of predators and whether these observed differences could explain variation in trapability between lakes.

Eight male and eight female *O. propinquus* were collected from Blue Chalk Lake and Bass Lake in early August 1980. Blue Chalk Lake contained no smallmouth, largemouth, or rock bass and no yellow perch. Its brown bullhead density index was 15% of the maximum for all the lakes before log transformation. We classified it as a low-predator lake. In contrast, Bass Lake's density indices for the above fish species as a percent of the untransformed maximum were 63, 54, 4, 37, and 2. The sum of the abundance indices for the three basses ranked fifth among the 19 lakes, and we regarded it as a high-predator lake. The mean cephalothorax length of crayfish from Bass Lake was 21.4 mm with a range of 18.8−26.9 mm; Blue Chalk animals averaged 22.79 mm, with a range of 19.8−27.2 mm. The means were not significantly different using a *t*-test. Prior to being tested, the crayfish were acclimated to test conditions for at least 48 h in flow-through tanks at 20°C and a photoperiod of 16 h light:8 h dark. They were fed Purina Trout Chow. We conducted these experiments in August and September 1980 when the males were in reproductive form (form I) (Capelli 1975).

The experimental tank (24 × 155 × 31 cm deep) was divided with black plastic panels into eight equal sections (24 × 19.3 × 31 cm deep). Eight crayfish were tested concurrently in separate chambers. By visually and tactually separating individuals, we minimized the effect that highly active animals could have on less-active tank mates. A single shelter (5 cm diameter × 10 cm long) rested on black gravel in each chamber. Red light from 40-W red light bulbs allowed the observer to see the crayfish during the dark period. Observations began 48 h after the animals had been placed in the test chambers.

We studied diel activity patterns by recording the time spent in each of four mutually exclusive behaviors by each



crayfish for 6 min/h. Observations were taken in consecutive 8-h periods for each group of eight crayfish. On day 1, crayfish were observed from 11:00 to 18:00, on day 2 from 19:00 to 02:00, and on day 3 from 13:00 to 10:00. Each animal was therefore observed for a total of 144 min. All observations were made in the absence of real or simulated predators.

We recognized four mutually exclusive crayfish behaviors: (1) locomoting: walking, climbing, vigorous digging, and swimming; (2) feeding/grooming: while stationary or walking very slowly; (3) concealed: more than 50% of the body concealed in the shelter; (4) motionless: remaining still, not feeding or grooming, with more than 50% of the body outside the shelter.

Results

Crayfish Trapability and Abundance

Consistent with the original survey that prompted this work, we obtained high crayfish catches only in lakes with low densities of smallmouth, largemouth, and rock bass (Fig. 1). Results of direct counts of crayfish by divers allowed us to determine quantitatively whether this pattern was produced in part by changes in crayfish trapability. For most lakes the number of crayfish found by divers predicted trap catches fairly well (Fig. 2A). However, four lakes (O1, O2, P2, and P5 in Fig. 2A) with relatively dense crayfish populations exhibited low trapability, indicated by relatively low trap catches compared with numbers counted during searches. In all four of these lakes the sum of the abundance indices of largemouth, smallmouth, and rock bass was above the median of these sums for all lakes.

To test more objectively the relationship between predator density and trapability of crayfish populations, we used a stepwise multiple linear regression to determine whether predator density indices could account for some of the residual variance in the relation between trap catches and search counts. The two lakes without bass were eliminated from the regression data set because their unusually high crayfish densities allowed them to dominate the regression so that patterns in the other lakes were not well described. The analysis therefore addressed how trapability changed when predator density varied from low to high. When yellow perch, rock bass, smallmouth bass, largemouth bass, and brown bullhead density indices were allowed to compete for maximum r^2 improvement in a stepwise regression of trap catches on search counts, perch entered first (Statistical Analysis System, PROC Stepwise) (SAS Institute, Inc. 1979). However, its regression coefficient was positive, indicating that crayfish trapability is relatively high in lakes where yellow

FIG. 2. (A) Relation between crayfish trap catches and the average number of crayfish found in five 3-min searches by divers in each lake during July 1980. Lakes M1 and M2, which lack bass, have been deleted (see text). (B, C, and D) Residuals of a least squares best fit for all points in Fig. 2A as a function of abundance indices (see Methods) for yellow perch (B), rock bass (C), and the sum of largemouth plus smallmouth bass (D). The residuals were used as an index of trapability. In Fig. 2C and 2D, the crayfish species composition in each lake is indicated as follows: △, *O. virilis*; □, *O. propinquus*; ●, *O. obscurus*; ○, *C. robustus*; ◐, *O. propinquus* and *C. robustus*; ★, no crayfish caught. Species that did not comprise at least 10% of the total crayfish catch are ignored in these designations. Pearson product-moment correlation coefficients (r) and probabilities of the correlation being nonsignificant (P) are specified in Fig. 2B, 2C, and 2D. Lake identifier codes are as in Fig. 1.

TABLE 1. Summary of stepwise linear regression of crayfish trap catches on search counts and density indices for rock bass, largemouth bass, smallmouth bass, brown bullhead, combined largemouth and smallmouth bass, and combined largemouth, smallmouth, and rock bass ($N = 17$). Search counts were forced to enter the regression first. Subsequently, the criterion for entry priority was maximum r^2 improvement (PROC Stepwise) (SAS Institute, Inc. 1979). Only the first four steps are shown.

No. of independent variables	Variable	Regression coefficient	F value	Probability	Multiple r^2
1	Search count	0.165	3.52	0.08	0.19
2	Search count	0.110	1.81	0.19	0.40
	Rock bass	−0.283	4.87	0.04	
3	Search count	0.135	2.48	0.14	0.44
	Rock bass	−0.310	5.60	0.03	
	Smallmouth bass	−0.167	0.96	0.34	
4	Search count	0.106	1.22	0.29	0.46
	Rock bass	−0.457	3.53	0.08	
	Smallmouth bass	−0.270	1.44	0.25	
	All bass	0.180	0.52	0.48	

perch were abundant (Fig. 2B). When perch were eliminated from the set of independent variables in the regression, rock bass density was the only variable that could significantly increase the explained variance (Table 1; Fig. 2C). It had a negative loading and raised the coefficient of determination from 19 to 40%. The sum of largemouth and smallmouth bass density indices was not well correlated with the residuals from the regression of trap catches on search counts (Fig. 2D), and the addition of two more fish variables only increased the coefficient of determination to 46%. Brown bullhead never significantly contributed to the regression.

Different crayfish species did not differ markedly in the degree to which their trapabilities change in response to the risk of fish predation (Fig. 2C and 2D). *Orconectes virilis*, *O. propinquus*, and *C. robustus* were all present in lakes having a wide range of predator densities. In addition, none of these species is consistently found in lakes either above or below the general trend line for all lakes.

As well as affecting trapability, do predators also have some negative effect on crayfish density? Crayfish density as measured by search counts was less strongly correlated with predator density than was trap catch. The Pearson correlation coefficient for search counts versus the summed abundance of all bass species was −0.29 (ns, Fig. 3A) compared with −0.59 ($P < 0.01$) for trap catches versus bass (Fig. 1). Correlations with rock bass abundance alone were −0.43 ($P = 0.06$) for search counts (Fig. 3B) and −0.48 ($P < 0.05$) for trap catches. Our diver search counts were probably less efficient in lakes with high predator density, where crayfish are more likely to be concealed (see below), than in lakes with low predator density. Thus, the correlation between predator density and search counts is likely to be negatively biased, leading to an overestimation of the effect of predators on crayfish density. We conclude that crayfish trapability was more strongly affected by predators than was crayfish abundance.

BEHAVIORAL BASIS FOR TRAPABILITY DIFFERENCES

Activity patterns of crayfish from lakes with both high and low bass densities (Fig. 4) showed lowest shelter occupancy and highest levels of locomotory and feeding/grooming behaviors during the night. However, many crayfish from Blue Chalk Lake (no bass) remained exposed and active during the day. Although most of these crayfish retreated to their shelters a few minutes after the lights went on, they generally emerged several hours later and resumed locomotion and feeding/grooming activities. In contrast, crayfish from Bass Lake (high bass abundance) generally remained inactive and concealed in the shelters during the day. When the lights came on, most exposed crayfish returned to their shelters within a few minutes and did not reemerge. Crayfish from both lakes apparently anticipated the onset of the artificially controlled darkness and dawn. The lights were turned off at 21:00 and on at 05:00, but crayfish began emerging from the shelters at 20:00 and, in the case of animals from Bass Lake, returning to them at 02:00. Crayfish from Blue Chalk Lake returned to their shelters at 04:00. Activity of *O. propinquus* may be endogenous in part and not maintained solely by environmental cues.

Crayfish from Blue Chalk and Bass lakes also differed in overall activity levels. Averaged over the entire 24-h period, Bass Lake crayfish spent significantly more time in shelters ($P < 0.05$) and less time locomoting ($P = 0.006$) than did Blue Chalk Lake animals. Probabilities are derived from a one-way analysis of variance using subprogram ONEWAY from the Statistical Package for the Social Sciences (SPSS) (Nie et al. 1975). These differences were also highly significant within both the day and the night periods (Table 2). As well, Bass Lake crayfish showed nonsignificant tendencies to spend more time motionless ($P = 0.36$) and less time feeding/grooming ($P = 0.07$) than crayfish from Blue Chalk Lake when behaviors were averaged

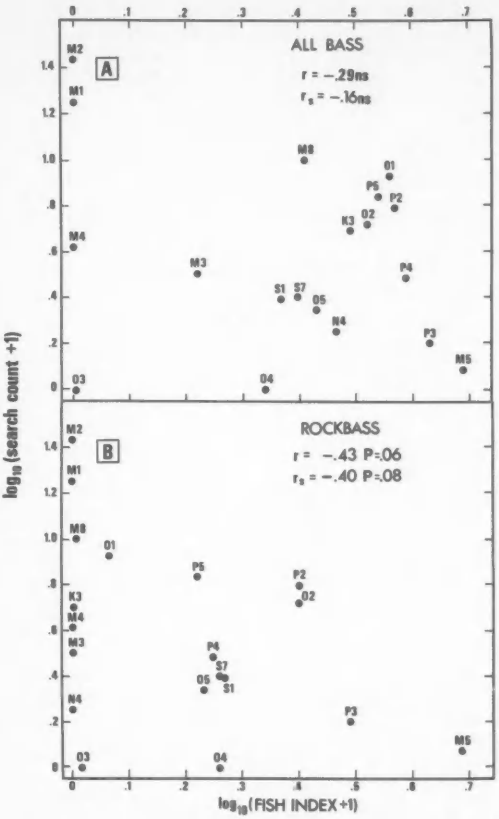


FIG. 3. Relations between crayfish density as represented by search counts and (A) the sum of largemouth, smallmouth, and rock bass abundance indices or (B) rock bass abundance index. Product-moment correlation coefficients are designated r and Spearman rank correlation coefficients are designated r_s.

over 24 h. When the day and night periods were considered separately, Bass Lake crayfish spent significantly more time motionless at night and less time feeding/grooming during the day than those from Blue Chalk Lake (Table 2). The two populations also differed in the degree of behavioral difference between males and females. In the Bass Lake group, males spent significantly less time in the shelters ($P < 0.01$), more time locomoting ($P = 0.013$), and more time performing maintenance behavior ($P < 0.01$) than did females. However, no significant behavioral differences between males and females from Blue Chalk Lake were detected.

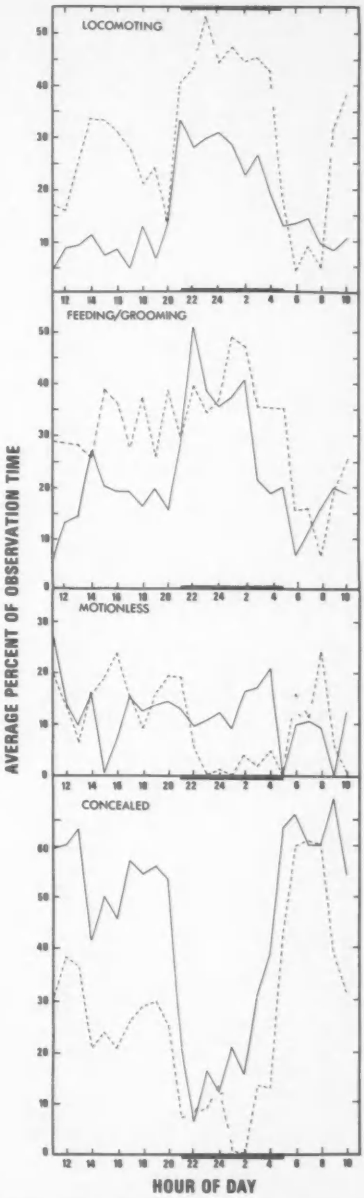


FIG. 4. Diel pattern of behavior in the laboratory for eight male and eight female *O. propinquus* from a lake with no smallmouth, largemouth, or rock bass (Blue Chalk Lake, broken line) and a lake with high bass density (Bass Lake, solid line). Heavy bar on the abscissa indicates the dark period. Data from each lake are combined results of two replicate experiments, each involving eight animals. Ninety-six minutes of observation was summarized in each point. Standard errors for each point were positively correlated with the mean; they ranged from 0.03 to 0.13.

TABLE 2. Average proportion (±SE) of time spent in four behavioral categories by 16 *O. propinquus* from Bass Lake (high bass density) and Blue Chalk Lake (no bass) during day and night periods in the laboratory arenas. Values for day are averages of the groups' performances for hours 6–20 ($N = 15$); those for night are averages of hours 22–4 ($N = 7$). Ninety-six minutes of observation were summarized in each hour's measurement. For each behavioral category, differences between day and night periods within lakes, and those between lakes for both the day and night periods are significant except where superscripted. Corresponding superscripts identify nonsignificant pairs.

		Locomoting	Feeding/grooming	Motionless	Concealed
Bass Lake	Day	0.099±0.008	0.165±0.015	0.146±0.017[ab]	0.591±0.029
	Night	0.276±0.018	0.364±0.048[c]	0.150±0.018[b]	0.209±0.043
Blue Chalk Lake	Day	0.229±0.030	0.276±0.026	0.134±0.022[a]	0.350±0.039
	Night	0.477±0.015	0.414±0.025[c]	0.026±0.009	0.082±0.023

Discussion

The relatively low catches of crayfish in traps set in lakes with high predator density are apparently caused both by reductions in the density of crayfish (Fig. 3) and changes in their behavior that reduce the effectiveness of passive traps. Dense crayfish populations can coexist with high predator densities (e.g. Bass Lake). In general, reduced trap catches at high predator densities seem to result more from reduced trapability than from reduced crayfish density.

One reason for this reduced trapability is restricted spatial distribution within a lake, the "microhabitat depression" effect defined by Charnov et al. (1976). We observed that crayfish burrows were not found on sand except in lakes with few or no bass. Thus, the resources in sandy habitat would be unavailable to crayfish in lakes with predators, and the total crayfish population in those lakes would be expected to be lower than if fish predators were absent.

Even within areas of good cover, however, predator-mediated behavioral changes would be expected to affect trapability. Stein and Magnuson (1976) documented reductions in activity and increased use of shelters by *O. propinquus* when smallmouth bass were introduced into their aquaria. We found that, even in the absence of a predator, *O. propinquus* from a high-bass lake were more strictly nocturnal, more shelter-bound, and generally less active than those from a lake lacking bass. These differences were significant during both the day, when most predators are active, and the night, when the crayfish are exposed to traps. In addition, male–female differences in behavior were significant only in the population that had been exposed to high bass densities, with males being less restricted to shelters and more active than females. This result is consistent with Stein and Magnuson's (1976) finding that females are more vulnerable to smallmouth bass predation than males with the same cephalothorax length. The mechanism by which the facultative, reversible behavior changes described by Stein and Magnuson (1976) become fixed responses that persist in the absence of immediate predation risk, such as those we recorded, is unknown. However, Strong (1972) demonstrated inheritable differences in mating behaviors of amphipod populations exposed to different predation regimes, and Arnold (1977, 1981) demonstrated a genetic component to differences in feeding behavior between garter snake populations.

The observed behavior changes are consistent with the reduced trap efficiency we found in lakes with abundant bass (Fig. 2). They also lead us to expect that sex ratios of trapped crayfish should be increasingly male biased as bass density increases, but our sample sizes are inadequate to test that hypothesis.

Although all the direct observations of predator-mediated behavior changes in crayfish have been done with *O. propinquus*, our survey results suggest that *C. robustus* and *O. virilis* also respond behaviorally to the risk of predation. For all these species, passive trap catches will not be a good measure of relative crayfish abundance among lakes whose predator populations vary. We are unable to evaluate the response of *O. obscurus* to predation risk because it was common in only one lake.

Our regression analyses indicated that various fish species have different effects on the trapability of crayfish. Yellow perch abundance indices are positively correlated with trapability (Fig. 2B), even though the larger size classes of yellow perch eat crayfish (Laarman and Schneider 1972; Keast 1977). However, young yellow perch are preyed upon by largemouth and smallmouth bass (Scott and Crossman 1973) and rock bass (Tester 1931). Perhaps crayfish experience reduced predation risk in lakes with dense perch populations because perch provide an alternative food source for predators. The regression analyses suggested that rock bass had more influence on trapability than smallmouth and largemouth bass. Nevertheless, *Micropterus* species were influential in at least one lake. Bass Lake, with high *Micropterus* densities and an almost insignificant rock bass population (see Methods), had a low trapability (Fig. 2A, lake O1) and supported a crayfish population with very different behavior patterns than those for lakes with no bass (Fig. 4).

Although the results of the multiple regression could reflect differing capabilities of fish species for preying on crayfish and thereby altering their behavior, Walter Momot (Lakehead University, Thunder Bay, Ont.) pointed out that differing responses of the fish species to our minnow traps could also produce the observed results. Our traps may have differentially attracted various bass species, which tend to station themselves around underwater objects. The areas around traps would therefore be less hospitable for crayfish in a lake with attracted fish species than in a lake with an equal density of unattracted ones. Consequently, we would expect differing trapabilities not because the two crayfish populations differed

in their activity patterns, but because crayfish around traps were responding to different local fish densities in the two lakes. We conclude that rock bass are particularly likely to reduce trapability of crayfish, and each of the three bass species is likely to have a negative effect on the availability of crayfish to the other two. However, whether rock bass has an unusually negative effect on availability as well as trapability cannot be determined from our data.

Our behavioral observations show that these diurnal and crepuscular feeding fish species produce significant reductions in nocturnal as well as diurnal crayfish activity. Thus, the behavioral resource depression (sensu Charnov et al. 1976) produced by the bass will also have negative effects on nocturnal predators such as the brown bullhead. In this case it appears that behavioral resource depression has an effect nearly as broad in time as if the crayfish had actually been eaten.

The fact that predator-induced behavior changes persist for at least 3 wk in the absence of predators suggests that interspecific comparisons of crayfish behavior patterns must be carefully controlled for differences in the predation risk of the populations being studied. For example, using two comparable laboratory behavior studies from the literature to infer that one species is more nocturnal than another (e.g. Stein and Magnuson 1976, p. 759) must now be considered inappropriate, unless the predation risks experienced by the subject populations are known to be similar. Accordingly, it is important that authors of future crayfish behavior studies describe the predation history of their source populations so that the influence of predation risk on their results can be assessed. These cautionary remarks probably have wide applicability to behavioral studies of other organisms, given that interpopulational behavioral differences related to predation risk have been observed in salamanders (Taylor 1983) and amphipods (Strong 1972; Robert L. Baker, University of Toronto, Erindale Campus, Ont., personal communication) as well as crayfish.

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Relationship Between Environmental Temperature and Yields of Subarctic and Temperate Zone Fish Species[1]

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SCHLESINGER, D. A., AND H. A. REGIER. 1983. Relationship between environmental temperature and yields of subarctic and temperate zone fish species. Can. J. Fish. Aquat. Sci. 40: 1829–1837.

Fishes inhabiting subarctic and temperate zone lakes exhibit distinct optimal growth temperatures and temperature preferenda. However, within regional data sets, attempts to correlate fish yields with temperature variables have generally been unsuccessful. In our study, curvilinear relationships between "long-term mean annual air temperature" (TEMP) and sustained yields of three species were fitted using data from 23 intensively fished lakes in Canada and the northern United States. Optimum TEMP values for sustained yield were approximately −1.0, 1.5, and 2°C, respectively, for lake whitefish (*Coregonus clupeaformis*), northern pike (*Esox lucius*), and walleye (*Stizostedion vitreum vitreum*). These differences suggest that the influence of temperature on sustained fish yields from subarctic and temperate zone lakes may, in the past, have been underestimated.

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Les poissons habitant les lacs des zones subarctiques et tempérées ont des températures de croissance optimales et exhibent des preferenda thermiques distincts. Cependant, dans des séries de données régionales, les efforts en vue d'établir une corrélation entre rendement en poisson et variables de température ont généralement échoué. Dans la présente étude, les relations curvilinéaires entre la « température de l'air annuelle moyenne à long terme » (TEMP) et les rendements soutenus de trois espèces ont été ajustés à l'aide de données provenant de 23 lacs intensivement pêchés au Canada et dans le nord des États-Unis. Les valeurs optimales de TEMP donnant un rendement soutenu sont d'environ −1,0; 1,5 et 2°C respectivement pour le grand corégone (*Coregonus clupeaformis*), le grand brochet (*Esox lucius*) et le doré (*Stizostedion vitreum vitreum*). Ces différences donnent à penser que l'influence de la température sur les rendements soutenus en poisson des lacs des zones subarctiques et tempérées peut avoir été sous-estimée dans le passé.

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REGRESSION equations for predicting potential fish yields from freshwater lakes and reservoirs have become common in the fisheries literature. Total fish yields have been correlated with surface area, mean depth, total dissolved solids, total and biologically available phosphorus, the morphoedaphic index (MEI), primary production, benthic standing crop, and fishing effort (Ryder 1965; Jenkins 1968; Jenkins and Morais 1971; Henderson and Welcomme 1974; Melack 1976; McConnell et al. 1977; Oglesby 1977; Matuszek 1978; Liang et al. 1981; Hanson and Leggett 1982; Schlesinger and Regier 1982; Youngs and Heimbuch 1982; McCombie 1983; Schlesinger and McCombie 1983).

Climate is a factor which can be viewed as having both a "controlling" and a "limiting" influence (Fry 1947) on potential fish yield (Fig. 1). However, attempts to correlate observed yields with climatic variables have met with limited success. Generally, the significance of yield/climate equations has tended to increase as the latitudinal range within the data set increases. For example, Schlesinger and Regier (1982) discovered that "long-term mean annual air temperature" (TEMP) was a significant predictor of sustained multispecies yields from commercial fisheries of 43 lakes covering a latitudinal range of 62°N to 15°S. In contrast, Matuszek (1978) found that the climatic variable "degree-days > 5.56°C" was not a significant predictor of sustained multispecies yields from commercial fisheries of 22 subarctic and temperate zone lakes located from 62°N to 42°N. Likewise, Schlesinger and McCombie (1983) were unable to fit a significant regression equation using sport fishing yields, effort, and TEMP data from 85 temperate

[1]This contribution is one of a sequential set of papers growing out of a special symposium on Large-Scale Comparative Studies of Aquatic Systems which was held at the June 1982 annual meeting of the American Society of Limnology and Oceanography in Raleigh, North Carolina.

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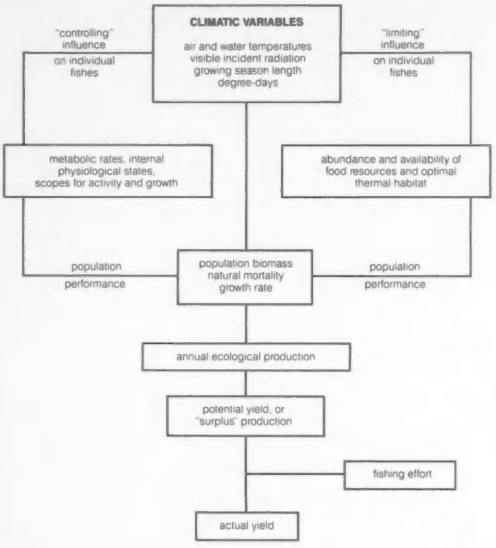

FIG. 1. Generalized scheme showing how climate ultimately influences fish yield, incorporating Fry's (1947) paradigm.

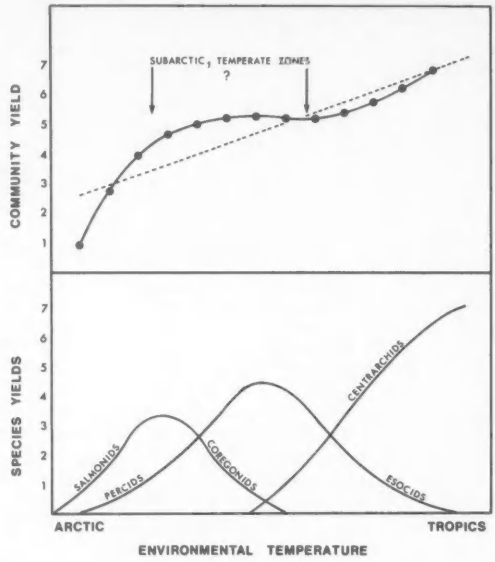

FIG. 2. Hypothetical relationship between potential fish yield and environmental temperature in subarctic and temperate zones. Units for fish yield are arbitrary. The upper panel shows the form of the curve when species from all families are being harvested at the same time (—). The points defining this curve could also be fitted with a linear least-squares regression line (---) which would be consistent with the results of our previous work (Schlesinger and Regier 1982). If the temperature range encompassed by earlier studies (Matuszek 1978; Schlesinger and McCombie 1983) is positioned as shown, then it becomes clear that fitting a significant community yield/environmental temperature equation would be difficult, given the sampling and estimation variances involved.

Ontario lakes located from 52°N to 39°N.

The studies of Matuszek (1978) and Schlesinger and McCombie (1983) suggest a temptingly simple interpretation; namely, that differences in environmental temperature among subarctic and temperate zone lakes are minor and have little impact on ecological fish production and potential yield. However, the ranges of environmental temperature within these data sets appear large enough to render this interpretation unlikely. An alternative hypothesis is as follows: Most subarctic and temperate zone lakes are dimictic and have greater variety of thermal habitats than lake types found at the extremes of latitude (Wetzel 1975). Consequently, fish species inhabiting subarctic and temperate zone lakes exhibit distinct thermal adaptations and achieve maximum levels of productivity and potential yield at different ambient temperatures. Since the response of a fish community to changes in temperature is a composite of the responses of individual species (Fig. 2), effects of differences in environmental temperature among subarctic and temperate zone lakes are probably significant, but perhaps can be detected more readily with respect to *species* yields, rather than *total* or *community* yield.

The purpose of this study was to investigate possible support for the above hypothesis by examining the fisheries literature. For our purposes, a "fish community" is defined simply as an aggregate of two or more species in a given lake, and "community yield" is the total yield of all species captured in a multispecies fishery.

Methods and Materials

The primary approach for investigating the species yield/environmental temperature hypothesis was to reexamine actual yield data. Using original sources of data, community yield estimates reported by Smith (1977) and Matuszek (1978), and by Schlesinger and McCombie (1983) were partitioned into species yield estimates, and regression analyses were performed using fishing effort, the morphoedaphic index (MEI = total dissolved solids/mean depth), and long-term mean annual air temperature (TEMP) as independent variables. TEMP was chosen as the climatic index because preliminary analyses showed it to be a better predictor of species yields than "degree-days > 5°C." Third- or fourth-order polynomials were fitted when the array of data points indicated that a curvilinear description would be appropriate. The Biomedical Computer Programs statistical package was used for this purpose.

When Ryder (1965) fitted his regression equation relating commercial fishing yields to the MEI, he used a data set comprised of lakes that had been moderately to intensively fished for a long period of time. Hence, potential yields calculated from Ryder's equation have come to be considered as estimates of maximum sustainable yield (MSY). However, there is no way of determining the extent to which these calculated potential yields, or the original yield

TABLE 1. Optimal growth temperatures and final temperature preferenda of commercial and sport fish species in subarctic and temperate zone lakes[a].

Species	Size or life stage	Optimal temperatures		Final preferenda	
		Growth[b]	Net biomass gain[b]	Mean	Range
		Cold Water			
Lake herring (*Coregonus artedii*)	larvae	18	16		
	large			9	7–10
Lake whitefish (*Coregonus clupeaformis*)	many sizes			14	12–17
Lake trout (*Salvelinus namaycush*)	many sizes			12	10–16
Brook trout (*Salvelinus fontinalis*)	fry, juvenile	15	15		
	adult	16	16		
	many sizes			17	8–20
Brown trout (*Salmo trutta*)	juvenile, adult	13			
	many sizes			14	12–18
Rainbow trout (*Salmo gairdneri*)	juvenile	17	17		
	many sizes			18	13–22
Grand mean		16	16	14	
		Cool Water			
Northern pike (*Esox lucius*)	juvenile	19			
	fry	26	21		
Muskellunge (*Esox masquinongy*)	small			24	
Grass pickerel (*Esox americanus*)	small			26	
Chain pickerel (*Esox niger*)	medium			24	
Walleye (*Stizostedion vitreum vitreum*)	juvenile	22	22		
	large			22	21–23
Sauger (*Stizostedion canadense*)	juvenile	22	22		
	large			19	
Yellow perch (*Perca flavescens*)	fry	28			
	juvenile	23			
	many sizes			20	7–27
Grand mean		23	22	23	
		Warm Water			
Bluegill (*Lepomis macrochirus*)	juvenile	31			
	juvenile	30			
	many sizes			30	27–32
Pumpkinseed (*Lepomis gibbosus*)	many sizes			28	24–32
Green sunfish (*Lepomis cyanellus*)	many sizes			29	27–31

TABLE 1. (*Concluded*).

Species	Size or life stage	Optimal temperatures: Growth[b]	Optimal temperatures: Net biomass gain[b]	Final preferenda: Mean	Final preferenda: Range
Rock bass (*Ambloplites rupestris*)	many sizes			25	21–30
Largemouth bass (*Micropterus salmoides*)	fry	28			
		25			
		27			
	many sizes			29	27–32
Smallmouth bass (*Micropterus dolomieui*)	juvenile	26[c]			
	many sizes			24	12–31
Grand mean		28		28	

[a]All values are water temperatures in °C. Temperature preferenda are from Cherry et al. (1977) and/or Coutant (1977). Optimal temperatures are from Strawn (1961), McCormick et al. (1971, 1972), Hokanson et al. (1973a, b), Horning and Pearson (1973), Elliott (1975), Koenst and Smith (1976), Hokanson (1977), Hokanson et al. (1977), Lemke (1977), Casselman (1978), Beitinger and Magnuson (1979), and Brett (1979).

[b]At maximum ration.

[c]Small number of fish per tank, compared with other test temperatures.

estimates, deviate from true MSY (W. C. Leggett, McGill Univ., personal communication).

Therefore, we have chosen to define the yield estimates of Smith (1977) and Matuszek (1978) as "sustained yields" (SY), with the understanding that SY values are inexact estimates of true MSY values.

Because of the extensive yield records for the lakes in Matuszek's (1978) data set, special consideration was given to the method of determining SY for individual species. Competitive and predator–prey interactions between fish species will affect population biomass and potential yield. As an example, consider lake trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus clupeaformis*). When the standing crop of a lake trout population is reduced by some stress (such as overfishing), whitefish biomass will probably increase as whitefish exploit former lake trout habitat and resources, and are released from predation by lake trout. A value for whitefish SY, calculated from a time interval following the collapse of the lake trout population, would probably be an overestimate of the whitefish SY expected from a lake with a stable fish community composition. To avoid this difficulty, SY estimates for lake trout, lake whitefish, northern pike (*Esox lucius*), and walleye (*Stizostedion vitreum vitreum*) were calculated from approximately the same time interval, prior to major changes in community composition, even though greater yields of particular species were sometimes taken following the decline of a coinhabitant.

For each lake, a time interval of 20–30 years was identified during which community composition was stable and community yield was at a maximum. Then, individual species SY estimates were calculated as the 15-yr average of maximum species yield within the community yield interval. For each lake, 15-yr time intervals for individual species SY calculations overlapped to some extent (Appendix 1). We have assumed that each species was in demand and readily marketable during the time interval from which SY was calculated.

One of the lakes in Matuszek's data set, St. Clair, was rejected from our data set because a large proportion of its commercial catches probably included migratory stocks from Lakes Erie and/or Huron (Ferguson and Derksen 1971). A walleye SY estimate from the Red Lakes, Minnesota, along with the relevant abiotic data (Smith 1977), was added to the analysis.

To expand the scope of the study, laboratory measurements of temperature preferenda and optimal growth temperatures were also used as indices of potential yield. Although fish in laboratories are generally subjected to less environmental variability than are fish in nature, comparing the results among laboratory studies can still be difficult because of differences in life stage, genetic characteristics of test fish, fish density per experimental unit, water quality, food quality, and photoperiod. Nonetheless, laboratory data at least provide a baseline comparison of the productive potential of different species at given water temperatures.

Estimates of ecological production of lake-dwelling fish populations (Johnson 1966; Chadwick 1976; Clady 1975; Carlander 1977; Mahon and Balon 1977; Chapman 1978; Power 1980) were not extensive enough to analyse meaningfully with respect to TEMP.

All fishes included in this study (Table 1) are of commercial or sport fishing value in subarctic and temperate regions of North America. Thermal groups have been recognized as those families adapted to cold, cool, and warm water conditions.

Results and Discussion

Optimal Growth Temperatures and Temperature Preferenda

The optimal growth temperature is that water temperature at which growth rate is maximized. Although variations with size and age do occur, this parameter is reasonably consistent within thermal groups (Table 1). Average optimal

TABLE 2. Original data of Matuszek (1978), with community SY partitioned into species SY, and including values for long-term mean annual air temperature (TEMP). Red Lakes data were taken from Smith (1977). Blank spaces indicate that the species was not harvested or that SY averaged less than 0.01 $kg \cdot ha^{-1} \cdot yr^{-1}$ and was, therefore, considered inconsequential. Asterisks indicate that catch records were incomplete (*) or that MSY was known to have been exceeded (**) (see Christie 1978). Values in parentheses were treated as outliers and were not included in the final statistical analyses.

Lake	Area (km)	MEI ($mg \cdot L^{-1} \cdot m^{-1}$)	TEMP (°C)	Species SY ($kg \cdot ha^{-1} \cdot yr^{-1}$) Lake trout	Lake whitefish	N. pike	Walleye
Great Slave	25382	2.2	−4.4	**	**	0.03	
Amisk	321	6.7	−0.4	0.04	2.77	0.10	0.08
Athabasca	7900	2.2	−3.3	0.35	0.32	0.02	0.02
Wollaston	2062	1.7	−5.2	0.77	0.61	0.03	0.02
Reindeer	5569	2.3	−5.2	0.35	0.54	0.03	0.02
Big Peter Pond	552	10.1	−0.6		**	0.90	**
Little Peter Pond	189	28.2	−0.6		**	1.72	**
Churchill	433	15.1	−0.6		1.02	1.22	0.40
Cree	1152	1.8	−2.3	0.63	*	*	*
La Ronge	1178	11.7	−0.8	0.11	1.65	0.05	0.13
Ile a la Crosse	446	22.6	−0.6		1.31	1.23	0.91
Erie	25690	7.9	9.4		(0.52)	0.02	(0.55)
Ontario	19477	1.8	8.1	0.16	(0.41)	0.06	0.02
Michigan	58016	1.6	7.7	0.56	0.21		
Superior	82414	0.4	3.9	0.23	(0.04)		
Huron (proper)	41659	1.8	6.6	0.36	0.25		0.16
North Channel	4550	3.9	5.4	0.56	0.23	0.08	0.11
Georgian Bay	13752	2.1	6.2	0.48	0.40	0.03	0.03
Rainy	858	5.8	2.2		0.66	1.12	1.40
Lake of the Woods	3569	11.7	3.3	0.02	0.37	0.55	0.83
Nipigon	4481	1.8	0.0	0.29	1.12		0.07
Red Lakes	1169	34.7	3.6				2.94

growth temperatures for fishes fed ad libitum are 16°C for coldwater species, 23°C for coolwater species, and 28°C for warmwater species.

The final temperature preferendum is that water temperature to which a fish will eventually gravitate regardless of its previous acclimation history (Fry 1947). Final temperature preferenda also vary with size and age. They appear to be reasonably consistent for coolwater and warmwater fishes, somewhat less consistent for coldwater fishes (Table 1). Final temperature preferenda average 14°C for coldwater species, 23°C for coolwater species, and 28°C for warmwater species.

These average values for optimal growth temperature and final preferendum are very similar to values calculated by McCauley and Casselman (1981), whose work we discovered after completion of our study.

Beitinger and Fitzpatrick (1979) suggested that the final temperature preferendum should coincide with the temperature at which key physiological, biochemical and life history processes of a species are optimized. The similarity between final temperature preferenda and optimal growth temperatures (at maximum ration) within species and thermal groups supports this idea, and suggests that these parameters are probably useful indices of water temperatures at which biomass accumulation and potential yield would be maximized under natural conditions.

Values for optimal growth temperatures (Table 1) were derived from fishes fed maximum rations, whereas fish populations in nature probably do not achieve maximum consumption rates very often. This is an important consideration, as the optimal growth temperature has been shown to decrease as ration size decreases (Brett 1979). Since a consistent relationship between ration size and selected temperature has yet to be established (Beitinger and Fitzpatrick 1979), it is not known if optimal growth temperatures and selected temperatures would be similar when food is limiting. Centrarchids appear to move to the extremes of their preferred temperature range when food is in short supply (Crowder and Magnuson 1982), and the work of Brandt et al. (1980) on thermal habitats and fish distribution in Lake Michigan suggests that when final temperature preferenda are available, each species will be found in greatest abundance at its preferendum (assuming adequate food availability). However, the interpretation of fish distribution in a varied thermal environment is difficult, owing to uncertainty about the primary factor(s) contributing to the observed distribution. "Thermal habitat partitioning" may be representative of true behavioral thermoselection, or it may be a composite response to temperature and other factors such as photoperiod, infection, predation, and life stage- or species-specific differences in food resource partitioning (Magnuson and Beitinger 1978).

SUSTAINED YIELD

In laboratory growth experiments, "net biomass gain" for a group of test fish is the total weight increase during the test interval minus the total weight loss due to natural

TABLE 3. Curvilinear equations predicting the relationships between species SY and mean annual air temperature (TEMP) in °C, calculated using the data of Smith (1977) and Matuszek (1978)[a]. These equations should only be used to predict species SY in the TEMP range of −5 to +9°C.

	Equation	r^2
1.	$\log_{10}$ lake whitefish SY = −0.0557 (TEMP) − 0.0168 ($TEMP^2$) + 0.0016 ($TEMP^3$) + 0.0488	0.677
2.	$\log_{10}$ northern pike SY = 0.2514 (TEMP) − 0.0646 ($TEMP^2$) − 0.0068 ($TEMP^3$) + 0.0010 ($TEMP^4$) − 0.1959	0.683
3.	$\log_{10}$ walleye SY = 0.3866 (TEMP) − 0.0558 ($TEMP^2$) − 0.0105 ($TEMP^3$) + 0.0011 ($TEMP^4$) − 0.4478	0.729

[a]A curvilinear fit to the log-transformed lake trout data was not possible. The linear equation was $\log_{10}$ lake trout SY = −0.0065 (TEMP) − 0.5974 (r^2 = 0.004).

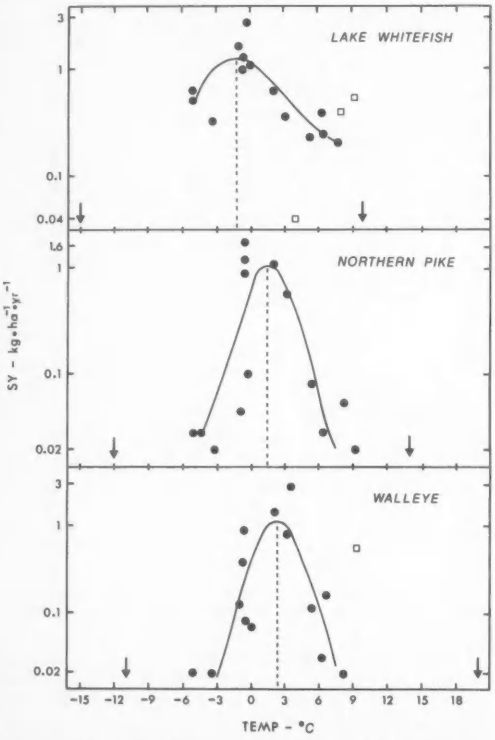

FIG. 3. The relationship between sustainable yield (SY) and long-term mean annual air temperature (TEMP) for three species, derived from data of Smith (1977) and Matuszek (1978). Squares represent points that were not included in the final curve-fitting. Arrows at the abscissae indicate the approximate TEMP range for native populations of each species.

mortality. Since there is no "fishing mortality" in these experiments, net biomass gain can be considered a laboratory index of potential yield. Optimal water temperatures for net biomass gain (potential yield) are 16°C for coldwater species and 22°C for coolwater species (Table 1). These values compare favorably with optimal growth temperatures and temperature preferenda.

Community yield estimates from 85 Ontario sport fisheries (Schlesinger and McCombie 1983) were partitioned into yields (kg/ha) of lake trout (n = 34 lakes), northern pike (n = 30 lakes), walleye (n = 42 lakes), and smallmouth bass (n = 48 lakes). TEMP ranges within each subset were 0.7−5.7°C for lake trout, 0.1−6.5°C for pike and walleye, and 1.9−6.5°C for smallmouth bass. None of the linear species yield/TEMP equations were significant (t-test, $P > 0.05$), and a typical hump-shaped curve could not be fitted to any of the species data. These results might have been due to inadequacy of the effort data. Since angling pressure on most of these lakes varied from minimal to moderate, we must first account for differences in effort before we can expect to discover any yield/TEMP relationship. However, unlike yield, effort could not be partitioned into species-specific values. Over- or under-estimates of effort actually directed toward particular species might have obscured any influence of environmental temperature, although this is obviously conjecture.

Community SY estimates from commercial fisheries on 23 large subarctic and temperate zone lakes in Canada and the United States (Smith 1977; Matuszek 1978) were partitioned into SY estimates for lake trout, lake whitefish, northern pike, and walleye (Table 2). Curvilinear SY/TEMP equations could be fitted for all species except lake trout (Table 3, Fig. 3). Prior to final curve-fitting, several "outliers" were rejected because their positions caused a third- or fourth-order polynomial curve to re-ascend in the range of 6−9°C, clearly a statistical anomaly related to the curve-fitting procedure. Rejection of these data points did not appreciably alter the characteristic TEMP optimum of any curve.

SY is associated with an optimum TEMP value of about −1°C for lake whitefish, 1.5°C for northern pike, and 2°C for walleye (Fig. 3). The −1°C and 1.5°C isotherms of TEMP in North America lie approximately in the middle of the geographical ranges of lake whitefish and northern pike, respectively. The 2°C isotherm lies in the northerly half of the walleye range.

Considering that the species SY estimates are unavoidably imprecise, the relative positions of the SY/TEMP curves (Fig. 3) reflect the hypothesized pattern (Fig. 2) reasonably well.

Native walleye populations occur in the southern United

TABLE 4. Significant (t-test, $P < 0.05$) linear regression equations involving the morphoedaphic index, calculated using data from Table 2. The MEI is expressed as total dissolved solids (mg/L) divided by mean depth (m).

	Equation	n	r^2
1.	$\log_{10}$ lake trout SY = -0.7668 ($\log_{10}$ MEI) -0.2998	14	0.401
2.	$\log_{10}$ lake whitefish SY = 0.6497 ($\log_{10}$ MEI) -0.6683	17	0.492
3.	$\log_{10}$ northern pike SY = 1.4163 ($\log_{10}$ MEI) -1.9393	16	0.606
4.	$\log_{10}$ walleye SY = 1.3829 ($\log_{10}$ MEI) -1.8136	16	0.691

States where TEMP approaches 20°C. Therefore, the walleye SY estimate from Lake Erie may not be an outlier, and the TEMP optimum for walleye SY may, in fact, be greater than 2°C. Note, however, that any presumed upward shift in the TEMP optimum for walleye SY would reinforce the apparent species-specific differences (Fig. 3).

Matuszek (1978) found that the MEI accounted for 63% of the variability in community SY for these lakes. The MEI is also a significant predictor of species SY (Table 4). Deviations of observed species yields from MEI-predicted species yields are a measure of the yield variability left unexplained by the MEI. When these deviations were plotted against TEMP, curvilinear patterns similar to those shown in Fig. 3 emerged (data not shown here). Thus, the correlation between species SY and TEMP can be distinguished even after the effects of mean depth and total dissolved solids have been removed.

A primary difficulty in this study is relating TEMP (air temperature) to the effective environmental temperature of fishes (water temperature). Most lakes in the subarctic and temperate zones are dimictic and, on a yearly basis, there are strong positive correlations between TEMP and mean epilimnetic temperature, and between TEMP and mean hypolimnetic temperature (Brylinsky 1980). However, the thermal strata within a dimictic lake will not respond at the same rate with a given change in air temperature.

Differences in temperature response rates among thermal habitats help explain differences in the shapes of the SY/TEMP curves (Fig. 3). For example, the apparent compensatory nature of the whitefish SY/TEMP curve (i.e. flattened) may represent an artifact introduced by the use of TEMP as an index of mean annual thermal experience. Over the latitudinal zone of habitation examined in this paper, lake whitefish probably experience a more tempered annual thermal regime than either northern pike or walleye. As a generalization, all three species can select nearly optimal thermal habitat in dimictic lakes during the summer; lake whitefish are most likely to be found in the cold hypolimnion, whereas pike and walleye inhabit warmer metalimnetic and epilimnetic waters. However, on short time-scales (day, week, month), the temperature of the hypolimnion will change very little and slowly, while the epilimnetic temperature will fluctuate to a much greater extent (McCombie 1967). As a consequence, pike and walleye will have to expend more energy and time during the summer while searching for preferred temperatures. During winter, prevailing water temperatures (0–4°C) are much closer to the physiologically optimal temperature range of lake whitefish. Therefore, the flatness of the lake whitefish curve (Fig. 3) is consistent with the idea that because of their summer habitat and their lower optimal temperature range, whitefish in dimictic lakes are comparatively well-buffered against variations in atmospheric conditions.

Empirical methods can be used to relate TEMP to water temperature. When "weighted mean annual surface water temperature" values were calculated (Shuter et al. 1983) and plotted against species SY values for the lakes in Table 2, the curvilinear correlations were almost identical to those in Fig. 3, and optimum values for weighted mean annual surface temperature were approximately 5, 6, and 6.5°C, respectively, for lake whitefish, northern pike, and walleye. The curves are similar because TEMP is the major independent variable in the equations reported by Shuter et al. (1983). In the absence of extensive water temperature data, this is a reasonable procedure for estimating "environmental" temperature for epipelagic or littoral zone fishes.

SUMMARY

Water temperature patterns, and the volume of optimal thermal habitat available to different species at any point in time, will vary with lake morphometry, life stage of fishes, and social interactions within the fish community. The statistically recognizable influence of these factors, relative to the influence of environmental temperature, should gradually increase as regional disparities in climate decrease. Since species SY/TEMP curves could not be fitted using Schlesinger and McCombie's (1983) regional data, the hypothesis that "temperature differences within the subarctic and temperate zones have little impact on potential yield" cannot be rejected. Nonetheless, the reanalysis of Matuszek's (1978) data on a species level supports the alternative hypothesis (Fig. 2), and apparent species-specific differences in optimal TEMP values for SY (Fig. 3) suggest real changes in availability of optimal thermal habitat with changes in air temperature. Species-specific adaptations and responses to environmental temperature at least partially explain why climatic variables have not been successful predictors of community fish yields from data sets including only subarctic and temperate zone lakes.

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Appendix I

Time intervals from which species MSY values were calculated for the lakes listed in Table 3.

Lake	Time intervals			
	Lake trout	Lake whitefish	Northern pike	Walleye
Great Slave			1951–65	
Amisk	1941–55	1941–55	1941–55	1941–55
Athabasca	1951–65	1951–65	1957–71	1955–69
Wollaston	1957–71	1959–73	1960–74	1957–71
Reindeer	1955–69	1957–71	1960–74	1960–74
Big Peter Pond			1951–65	
Little Peter Pond			1946–60	
Churchill		1941–55	1941–55	1941–55
Cree	1954–68			
La Ronge	1960–74	1957–71	1960–74	1960–74
Ile a la Crosse		1955–69	1960–74	1957–71
Erie		1928–42	1919–33	1930–44
Ontario	1914–28	1915–29	1913–27	1921–35
Michigan	1911–25	1921–35		
Superior	1919–33	1914–28		
Huron (proper)	1923–37	1923–37		1925–39
North Channel	1925–39	1924–38	1924–38	1924–38
Georgian Bay	1924–38	1925–39	1923–37	1923–37
Rainy		1924–38	1924–38	1924–38
Lake of the Woods	1924–38	1929–43	1924–38	1924–38
Nipigon	1918–32	1918–32		1926–40
Red Lakes				1935–49

Empirical Predictors of Annual Surface Water Temperature Cycles in North American Lakes[1,2]

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Annual surface water temperature cycles of temperate zone lakes can be adequately described by a symmetrical sine wave of distinct amplitude and duration. The relationships between these sine wave components and climatic and morphometric variables were analyzed for 87 lakes spread over most of North America, and for 25 lakes located in south-central Ontario, Canada. Multiple regression equations are reported which permit estimation of the maximum annual surface water temperature (amplitude: AP) and the number of ice-free days (duration: DR) for a specific lake from data on long-term mean annual air temperature (TEMP), mean depth ($\bar{Z}$), and fetch (FT). These estimates can be used to calculate mean surface water temperature for just the ice-free period or for an entire year.

SHUTER, B. J., D. A. SCHLESINGER, AND A. P. ZIMMERMAN. 1983. Empirical predictors of annual surface water temperature cycles in North American lakes. Can. J. Fish. Aquat. Sci. 40: 1838–1845.

On peut décrire adéquatement les cycles annuels de température de l'eau de surface des lacs des zones tempérées à l'aide d'une vague de sinus symétrique d'amplitude et de durée distinctes. Les relations entre les composantes de cette vague et les variables climatiques et morphométriques ont été analysées dans 87 lacs répartis dans presque toute l'Amérique du Nord et 25 lacs situés dans le centre-sud de l'Ontario, au Canada. Nous présentons ici des équations de régressions multiples permettant d'estimer la température annuelle maximale de l'eau de surface (amplitude : AP) et le nombre de jours où un lac particulier est libre de glace (durée : DR). Ces équations ont été établies à partir de données sur la température de l'air annuelle moyenne à long terme (TEMP), la profondeur moyenne ($\bar{Z}$) et le fetch (FT). Ces estimations peuvent être utilisées dans le calcul de la température moyenne de l'eau de surface, soit seulement pour la période sans glace, soit pour une année entière.

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INDICES of the thermal environment of lake-dwelling organisms are useful predictors of many biological phenomena, ranging from year-to-year variations in the reproductive success of individual fish populations (MacLean et al. 1981) to lake-to-lake variations in the annual production of algal and fish communities (Brylinski and Mann 1973; Brylinski 1980; Schlesinger and Regier 1982). Thermal indices based on air temperatures (e.g. degree days >5°C, Colby and Nepszy 1981; long-term mean annual air temperature, Schlesinger and Regier 1982) have generally been used in such studies. Improved predictions might be achieved by using more precise descriptors of annual lake water temperature cycles.

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[2]This contribution is one of a sequential set of papers growing out of a special symposium on Large-Scale Comparative Studies of Aquatic Systems which was held at the June 1982 annual meeting of the American Society of Limnology and Oceanography in Raleigh, North Carolina.

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TABLE 1. Summary of data on the 87 lakes in the continental data set and the 25 lakes in the LEWG data set. Mean (mn), range (rg) and number of observations (*n*) are given for each variable. Within each data set, lakes have been subdivided into groups based on the presence (S) or absence (NS) of a well-defined period of summer thermal stratification. The third group (U) in the continental data set is made up of lakes which could not be classified as either S or NS, because of a lack of information in the original reference. A complete list of references for the continental data set is given below the table.

Variable		Continental data set			LEWG data set	
		S	NS	U	S	NS
AP (°C)	mn	22.1	17.3	18.0	24.3	24.9
	rg	12.0, 29.0	3.8, 25.0	11.1, 23.5	22.3, 25.2	24.1, 26.0
	n	52	21	14	21	4
DR (days)	mn	246	170	316	—	—
	rg	113, 365	54, 273	132, 365	—	—
	n	41	11	7	—	—
TEMP (°C)	mn	5.1	−1.3	1.6	5.1	5.7
	rg	−5.6, 10.1	−16.2, 7.4	−5.6, 7.7	4.4, 6.0	4.6, 6.2
	n	52	21	14	21	4
$\bar{Z}$ (m)	mn	13.3	10.4	24.6	8.9	2.0
	rg	1.8, 69.2	1.0, 40.4	8.2, 69.5	3.5, 20.1	0.9, 3.5
	n	52	21	14	21	4
THMZ (m)	mn	9.24	—	—	8.5	—
	rg	3.2, 30.0	—	—	4.3, 15.0	—
	n	52	—	—	21	—
FT (km)	mn	7.4	17.9	35.0	2.9	2.3
	rg	0.2, 47.9	0.6, 170.0	6.0, 108.0	0.9, 6.9	0.9, 3.7
	n	52	21	14	21	4
AR (km^2)	mn	16.2	455	837	3.0	2.5
	rg	0.03, 104.0	0.1, 7900	3.9, 5569	0.3, 11.4	0.3, 5.4
	n	52	21	14	21	4
VOL (km^3)	mn	0.33	10.5	15.2	28.3	6.1
	rg	0.0001, 3.2	0.0002, 205	0.13, 95.0	2.6, 136.0	0.7, 18.8
	n	52	21	14	21	4
EL (m)	mn	380	517	391	517	267
	rg	9, 2320	15, 1990	247, 777	189, 335	219, 373
	n	52	21	14	21	4
LATITUDE	rg	41°N, 64°N	43°N, 75°N	50°N, 64°N	44°N, 46°N	44°N, 46°N

LIST OF REFERENCES: Anderson (1970); Aulenback et al. (1978); Bannister and Bubeck (1978); Brett (1950); Brunskill and Schindler (1971); Carl (1953); Culver (1975); Duthie and Carter (1970); Eaton and Kardos (1978); Harman and Sohacki (1978); Harvey and Coombs (1971); Hobbie (1961); Johnson (1962, 1972); Kerekes (1974); LaPerriere et al. (1975); Larson (1972); McCombie (1967); Moeller (1975); Neess and Bunge (1956); Rawson (1936, 1942, 1960); Ricker (1937); Scheffer and Robinson (1939); Schindler (1971); Schindler and Nighswander (1970); Schindler et al. (1973, 1974a, b); Smith (1952); Stockner and Northcote (1974); Wetzel (1973).

Many workers (Dutton and Bryson 1960; McCombie 1967; Straskraba 1980) have shown that the basic pattern of annual surface water temperature cycles in lakes is adequately described by a sine wave. Furthermore, Shuter et al. (1980) showed that the components of the sine wave characteristic of a specific lake can be roughly estimated from mean summer air temperature, and that annual temperature regimes estimated in this way can be coupled to the known temperature preferences of an individual fish species (smallmouth bass, *Micropterus dolomieui*) to assess geographic variations in growth rate and timing and success of reproduction.

Our objective in this study was to develop regression equations for North American lakes which could be used to predict water temperature variables from climatic and morphometric variables. Such equations would also provide a succinct description of the effects of both climate and morphometry on annual lake temperature cycles.

Methods

Our efforts were focused primarily on the analysis of the following data sets: a continental data set comprising 87 lakes spread over a large part of North America (41−75°N); a regional data set (44−46°N latitude) comprising 25 of the lakes studied by the Lake Ecosystem Working Group (LEWG) at the University of Toronto (Table 1). The continental data set was compiled from reports in the scientific literature (sources: Table 1). Variables relating to the surface water temperature cycle of individual lakes were generally obtained from depth-time isotherm diagrams for one complete annual cycle. Morphometric data were given or could be calculated. Climatic data for each lake were obtained from Wernstedt (1972) or Environment Canada (1975). Data for the LEWG lakes consisted of temperature−depth profiles collected at biweekly intervals from spring through fall. Three

TABLE 2. Summary of data on the magnitude of year-to-year variation in annual water temperature cycles for four bodies of water in southern Ontario. The mean (mn), standard deviation (SD) and number (n) of cycles examined are given for both the maximum daily mean surface water temperature (AP) and the number of ice free days (DR).

Water body	Location	TEMP (°C)	$\bar{Z}$ (m)	AP (°C)			DR		
				mn	SD	n	mn	SD	n
Lake Opeongo	46°N 78°W	3.7	14.8	23.2	1.1	13	188	10.3	11
Lake-on-the-Mountain	44°N 77°W	7.5	9.5	26.1	1.7	11	244	16.7	9
South Bay, Lake Huron	46°N 82°W	5.2	18.2	—	—	—	237	10.1	25
Baie du Dore, Lake Huron	44°N 81°W	7.7	2.0	23.8	1.4	10	—	—	—

TABLE 3. Regression equations for predicting DR for the continental data set ($n = 59$). All coefficients are significantly ($P < 0.05$) different from zero. The fit of each regression equation to the data is summarized by two quantities: the square of the multiple correlation coefficient (r^2: fraction of the overall variation in ln DR that is accounted for by the regression); the standard deviation of the residuals (SD). The SD value is used to construct confidence intervals for predicted values of ln DR; given a set of values for the independent variables which lie near the middle of their observed ranges (Table 1), a 70% confidence interval for ln DR is approximately ($\ln DR_{pred} \pm SD$).

	Equation	r^2	SD
1.	$\ln DR = 0.0624\ (TEMP) + 5.168$	0.875	0.141
2.	$\ln DR = 0.153\ (\ln \bar{Z}) + 5.056$	0.131	0.372
3.	$\ln DR = 0.06\ (TEMP) + 0.073\ (\ln \bar{Z}) + 5.005$	0.904	0.125
4.	$\ln DR = 0.0615\ (TEMP) + 0.0318\ (\ln FT) + 5.129$	0.890	0.134

years of water temperature data (1978–80) were available for each lake, and variables relating to the surface water temperature cycle of each lake were averaged over these years. Morphometric data were provided by LEWG participants (Zimmerman et al. 1983). Climatic data were obtained from Environment Canada (1978, 1979, 1980).

Data from Crater Lake in Oregon (Byrne 1965) was originally included in the continental data set. Preliminary analyses showed it to be an extreme outlier from many of the regression equations fitted to the data. Its great mean depth (325 m) and unusual morphometry also set it apart from the rest of the lakes. For these reasons, it was excluded from the data set.

Since water temperature cycles for the lakes in the continental and LEWG data sets were characterized by averages based on, at most, 3 yr of data, reliable information on year-to-year cycle variation within lakes could not be extracted from them. To obtain a rough estimate of the magnitude of such variation, several years of annual temperature cycle data from two lakes and two partially enclosed bays were also analyzed (Table 2). These data consisted of daily mean surface water temperatures, calculated from recording thermograph data (Shuter et al. 1980), and estimated dates of freeze-up and ice break-up. All four water bodies are located in the same geographic area as the LEWG lakes.

SELECTION OF VARIABLES AND DATA ANALYSIS

Following Shuter et al. (1980), two descriptors of annual surface water temperature cycles were used as the dependent variables: the maximum surface water temperature reached during the annual cycle (amplitude: AP, °C); the duration of the ice-free part of the annual cycle (duration: DR, days). In the continental data set, DR values were estimated from depth-time isotherm diagrams which explicitly identified the periods of ice cover. Since investigators rarely reported the exact criteria used in specifying dates of ice appearance and disappearance, we could not precisely define the limits of our estimates of DR. No DR estimates were available for the LEWG data set.

Seven independent variables were used in the analysis. Each of these fell into one of two groups, depending on the mechanism through which it might link to water temperature. Group 1 consisted of long-term mean annual air temperature (TEMP, °C: taken from the meteorological station nearest each lake) and elevation (EL: m). These variables are associated with the input of heat to a lake. A positive effect of TEMP on both AP and DR was anticipated (Shuter et al. 1980). Group 2 consisted of mean depth ($\bar{Z}$, m), its components area (AR, km^2) and volume (VOL, km^3), and summer thermocline depth (THMZ, m: depth of the maximum vertical temperature gradient in the metalimnion), along with its correlate (Ragotzkie 1979; Arai 1981) fetch (FT, km: the maximum linear dimension of the lake). These variables are associated with the heat storage capacity of a lake. Anticipated effects included: positive effect of $\bar{Z}$ on DR; negative effect of $\bar{Z}$ on AP (Hutchinson 1957; Wetzel 1975; Straskraba 1980).

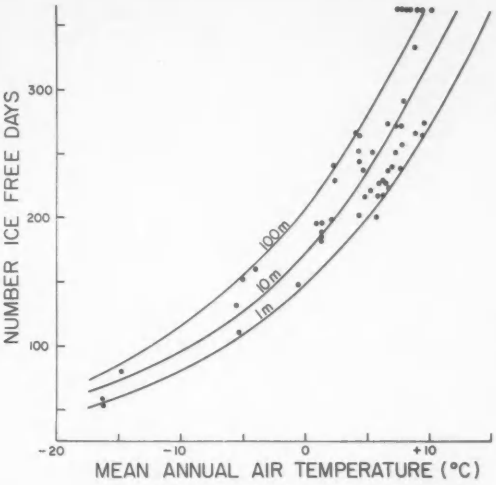

FIG. 1. Plot of annual number of ice-free days (DR) against mean annual air temperature (°C) for the continental data set. Data from all lakes with DR estimates are plotted. Some observations are hidden. The solid lines were derived from equation 3, Table 3 using values of 1, 10, and 100 m, respectively, for mean depth ($\bar{Z}$).

Analysis of each data set was carried out using the stepwise (BMDP2R) and the all-subsets (BMDP9R) multiple regression programs of the BMD statistical analysis package (Dixon and Brown 1979).

Results

Final results of the analysis of variation in DR for all lakes in the continental data set are summarized in Table 3 and Fig. 1. Since similar results were generated by a separate analysis using only those lakes exhibiting summer stratification, we concluded that the same regression equations were equally effective in describing the behaviour of DR in both types of lakes. Most of the observed variance in DR is accounted for by TEMP. A relatively small, additional amount is accounted for by heat storage variables, particularly $\bar{Z}$. There is no evidence that second order terms (e.g. $TEMP^2$, $(\ln \bar{Z})^2$) or interaction terms (e.g. TEMP × $\ln \bar{Z}$) would significantly improve the predictive power of the regression equations. TEMP and $\bar{Z}$ are positively related to DR, as expected. Since FT is positively correlated with $\bar{Z}$ ($r_{\ln FT \times \ln \bar{Z}} = 0.63$, $P < 0.01$), it is likely that its influence on DR reflects the same phenomenon which underlies the influence of $\bar{Z}$. Equation 4 (Table 3) is slightly inferior to equation 3 by the r^2 criterion, however, it is of practical interest because it can be used with information readily obtained from meteorological reports and maps. More detailed knowledge of individual lakes is required to use equation 3.

The analysis of variation in AP proceeded in stages. The LEWG and continental data sets were separated into groups, based on the presence (S lakes) or absence (NS lakes) of summer thermal stratification. Three of these groups (LEWG - S lakes; continental - S, NS lakes) contained sufficient data to permit them to be analyzed separately. Results from the two groups of S lakes were similar: (1) within groups, 3 equations containing both a heat input variable (TEMP) and a heat storage variable (one of ln THMZ, $\ln \bar{Z}$, or ln FT) each explained a significant amount of the observed variation in ln AP; (2) across the two groups, equations with the same independent variables had similar regression coefficients. These findings suggested that the data from these two groups of lakes could be pooled and analyzed together. Results from the group of NS lakes were different: (1) of the equations important among the S lakes, only the equation containing TEMP and $\ln \bar{Z}$ terms explained a significant amount of the ln AP variation observed in the NS lakes; (2) a comparison of this equation with the TEMP-$\ln \bar{Z}$ equation for S lakes revealed similar temperature coefficients, but significantly ($P < 0.05$) different $\ln \bar{Z}$ coefficients. These findings suggested that the NS lakes should be analyzed separately from the S lakes.

Given these results, two new data sets were formed: one consisting of all the S lakes from the LEWG and continental data sets; the other consisting of all the NS lakes. These two groups were then analyzed separately. The results of these analyses are presented in the first 4 columns of Table 4. The TEMP and $TEMP^2$ regression coefficients for the S and NS data are not significantly ($P > 0.05$) different from each other. This suggests that the heat input effect, as summarized in the variables TEMP and $TEMP^2$, is similar in both S and NS lakes. The $\ln \bar{Z}$ regression coefficient for NS lakes is similar to the ln THMZ coefficient for S lakes but significantly ($P < 0.05$) lower than the $\ln \bar{Z}$ coefficient for S lakes. This suggests that a relatively consistent measure of the heat storage effect for both S and NS lakes can be constructed by using the value of ln THMZ for S lakes and the value of $\ln \bar{Z}$ for NS lakes.

Given these results, all data from S and NS lakes were pooled and regression equations fitted using the following independent variables: TEMP, $TEMP^2$, TORZ (ln THMZ for S lakes, $\ln \bar{Z}$ for NS lakes), $TORZ^3$. Results of this analysis are summarized in the last two columns of Table 4. There is no evidence that interaction terms or higher order terms in TEMP or TORZ would significantly improve these regression equations. Equation 10 is slightly superior to equation 9 because of its higher r^2 value, and also because the distribution of its residuals more closely approximates a normal distribution. The behavior of equation 10 is illustrated in Fig. 2.

Use of either equation 9 or 10 for a stratified lake requires an estimate of the value of THMZ. In Table 5, we present the results of a regression analysis of the variation in THMZ observed in our data. Most of the observed variation in THMZ is accounted for by FT. Relatively small additional amounts are accounted for by $\bar{Z}$ and TEMP. The distribution of residuals is approximately normal for all equations. Separate analyses of the stratified lakes from the LEWG and continental data sets revealed relationships between ln THMZ and ln FT which were identical to each other and to the relationship reported by Arai (1981) for 36 Japanese lakes (Fig. 3). The similarity of this relationship, for three independent sets of data collected from widely separate geographic areas,

TABLE 4. Regression analysis of variation in AP observed in stratified (S) and nonstratified (NS) lakes. Each regression equation is identified by a number given under the data set name. The dependent variable for each equation is ln AP. The number of observations used (n), the value of each regression coefficient (cf), and its standard error (SE) are given. The fit of each equation to the data is summarized by the square of the multiple correlation coefficient (r^2) and the standard deviation of the residuals (SD).

	NS lakes	S lakes			S and NS lakes	
	5	6	7	8	9	10
n	25	73	73	73	98	98
Intercept	3.218	3.257	3.152	2.999	3.158	3.059
(SE)	(0.091)	(0.061)	(0.044)	(0.026)	(0.047)	(0.027)
Heat Input Variables						
TEMP	0.0264	0.0365	0.0359	0.0385	0.0437	0.0422
(SE)	(0.010)	(0.006)	(0.006)	(0.007)	(0.003)	(0.003)
$TEMP^2$	−0.0028	−0.0017	−0.0011	−0.0015	−0.0020	−0.0020
(SE)	(0.0008)	(0.0007)	(0.0007)	(0.0008)	(0.0003)	(0.0003)
Heat Storage	ln $\bar{Z}$	ln THMZ	ln $\bar{Z}$	ln FT	TORZ	$(TORZ)^3$
Variable						
cf	−0.170	−0.130	−0.081	−0.031	−0.108	−0.010
(SE)	(0.038)	(0.026)	(0.016)	(0.010)	(0.020)	(0.0014)
r^2	0.904	0.536	0.526	0.441	0.823	0.850
SD	0.167	0.104	0.105	0.114	0.135	0.124

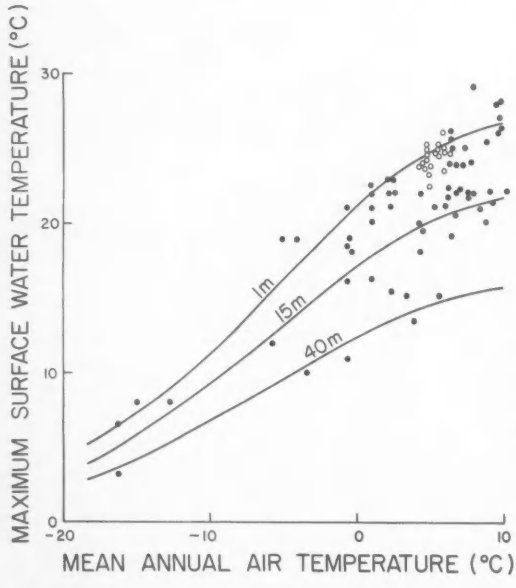

FIG. 2. Plot of maximum surface water temperature (AP, °C) against mean annual air temperature (°C) for the continental (●) and LEWG (○) data sets. Some observations are hidden. Lakes with unknown summer temperature–depth relations are not included. The solid lines were derived from equation 10, Table 4 using values of 1, 15, and 40 m, respectively, in the variable TORZ — ln THMZ for stratified lakes, ln $\bar{Z}$ for nonstratified lakes.

suggests that equation 11 can be generally used to provide unbiased estimates of THMZ.

Discussion

The findings from our empirical analysis of annual temperature cycles in North American lakes are consistent with the physical principles which govern lake heat budgets, and with other empirical studies. In general, an increase in the annual input of heat to a lake should lead to an increase in both DR and AP. Both of these effects were strongly evident in our data set. Given the same annual heat input, a lake with a greater mean depth should be able to store more of that heat than a shallower lake. The deeper lake will tend to freeze later than the shallower lake and, if deep enough, may not freeze over at all (Ragotzkie 1979). This effect was also evident in our data set. Differences in heat storage capacity will also affect AP. Given the same heat content, a lake with a greater heat storage capacity will store that heat in a greater volume of water at a lower temperature than a shallower lake. In lakes which exhibit summer stratification, the summer thermocline depth serves as a measure of summer heat storage capacity. In nonstratified lakes, the mean depth provides a similar measure of heat storage capacity (Ragotzkie 1979). Our findings are consistent with both of these principles. Strong negative relations between AP and various measures of heat storage capacity were noted. In addition, we found that the most consistent measure of this effect on AP was given by a composite variable obtained by using the summer thermocline depth for stratified lakes, and the mean depth for nonstratified lakes. Other empirical studies reporting similar findings include the global analysis of AP variation by Straskraba (1980) and the regional analysis of summer surface water temperatures by Webb (1978).

TABLE 5. Regression equations for predicting THMZ for stratified lakes in the LEWG and continental data sets ($n = 73$). All coefficients are significantly ($P < 0.05$) different from zero. The fit of each regression equation to the data is summarized by two quantities: the square of the multiple correlation coefficient (r^2); the standard deviation of the residuals (SD).

Equation	r^2	SD
11. ln THMZ = 0.298 ln FT + 1.82	0.662	0.284
12. ln THMZ = 0.217 ln FT + 0.214 ln $\bar{Z}$ + 1.42	0.718	0.262
13. ln THMZ = 0.301 ln FT − 0.0265 TEMP + 1.95	0.693	0.273
14. ln THMZ = 0.220 ln FT + 0.213 ln $\bar{Z}$ − 0.0263 TEMP + 1.550	0.748	0.250

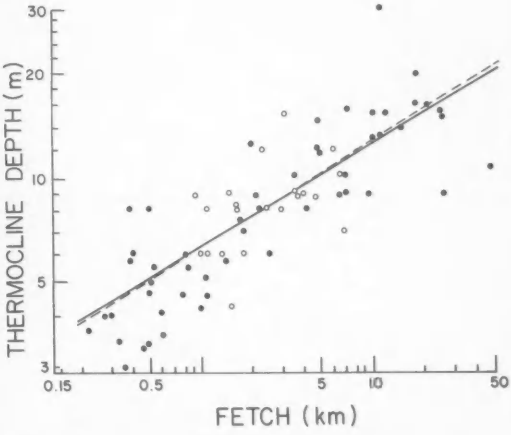

FIG. 3. Plot of summer thermocline depth (THMZ, m) against fetch (FT, km) for the continental (●) and LEWG (○) data sets. The solid line is the least squares regression line (no. 11, Table 5) for both data sets pooled. The dashed line is the relation derived by Arai (1981) from data on a set of 36 Japanese lakes with a similar range of values for both the thermocline depth and the fetch.

Our results on the empirical relation between thermocline depth and fetch are similar to the results reported in four of the six related studies summarized by Straskraba (1980). They differ significantly from the results in the remaining two studies (both of sets of lakes outside North America), and from the relationship reported by Ragotzkie (1979) for a number of lakes in central North America. Since the relationship we report is based on a more extensive data set ($n = 73$ vs. $n = 18$) covering a wider geographic area than that reported by Ragotzkie, it may be more representative of the average relationship for small to moderate size North American lakes. Straskraba (1980) presents convincing evidence that relationships of this sort seriously overestimate the thermocline depth of very large lakes (FT > 100 km). He suggests that it is more realistic to assume that the thermocline depth of freshwater lakes has an upper limit in the range from 20 to 25 m. This should be taken into consideration when using equations 11 through 14 to estimate the thermocline depth.

The equations presented in Tables 3 and 4 can be used to estimate DR and AP from meteorological and morphometric information. An approximate measure of the precision of an estimate, derived from one of these equations, can be calculated from the standard deviation (SD) of the residuals for that equation. For equations 3, 4, 9, and 10, SD values range from 0.124 to 0.135. Thus, for these equations, 70% confidence intervals for an estimate will range from about 87% of the estimated value to about 113%. This measure of precision should hold for the situation where the equations are used, as written, to estimate values of DR and AP for a specific lake in a specific year. If the equations are used to estimate long-term average values for DR and AP for a specific lake, or if the average annual air temperature for a specific year is used (instead of TEMP) to estimate the DR and AP values for a specific lake in that year, we would expect the confidence intervals to be somewhat narrower. This statement is based on the following argument. One component of the residual variation for each equation is the random, year-to-year variation in DR and AP associated with individual lakes. Reference to Table 2 shows that this kind of variation is substantial (standard deviation ≈ 5.5% of mean) for both DR and AP. In addition, simple regression analysis of the data summarized in Table 2 showed that a significant ($P < 0.05$) percentage (~25%) of the variation in both DR and AP could be accounted for by year-to-year variations in the annual average air temperature. Thus, we would expect mean DR and AP values based on TEMP, or yearly DR and AP values based on annual average air temperatures to be estimated more precisely than yearly DR and AP values based on TEMP. When equation 9 or 10 is used with an estimate of thermocline depth to obtain an AP estimate for a specific lake in a specific year, that estimate of AP will be less precise than indicated by the SD value for the appropriate equation. The uncertainty associated with the estimate of thermocline depth will reduce the precision of the AP estimate.

The equations presented in Tables 3, 4, and 5 can be used to estimate quantities which define the surface water temperature cycle of a lake during its ice free period:

$$T(t) = (\mathrm{AP} - A_o) \sin\left(\frac{\pi \cdot t}{\mathrm{DR}}\right) + A_o$$

where: $T(t)$ is the surface water temperature on day t; t varies from 1 to DR, with day 1 taken as the date of ice break-up in the spring and day DR taken as the date of ice formation in the fall; AP and DR are as previously defined; A_o is the surface water temperature during ice cover. This, in turn, permits calculation of a number of simple water temperature statistics, such as the mean surface water temperature during the ice free period (T'),

$$T' = 0.637\ AP + 0.363\ A_o$$

and the annual mean surface water temperature (T''),

$$T'' = \frac{DR \cdot T' + (1 - DR) \cdot A_o}{365}$$

Acknowledgments

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Synopsis and Classification of Living Organisms. *Sybil P. Parker [ed. in chief]. McGraw-Hill, New York. 1982. 2 vol., xviii, 1166 and 1232 p., illus. $179.40.*

This massive (6.5 kg) work is an attempt to provide synoptic descriptions of taxa down to family level, for all living organisms. Some 174 contributors worked with 14 consultants in writing 8200 synoptic articles. Few major groups were missed. Collembola, Protura, and Diplura were all omitted, perhaps due to differing interpretations of their affinities with the Apterygota. Vestimentiferans are only briefly mentioned by the author of the pogonophoran section because he considered them as annelids. Omissions of recently established higher taxa, Remipedia among crustaceans, Aphanoneura among annelids, may reflect delays between submission of articles and publication.

Treatment at the family level typically varies from a simple listing to a 500-word characterization. In a few cases families are totally omitted. Only 37 of the 145 families of oribatid mites are listed. The author of this section notes that classification at the family level is in need of revision and he perhaps excluded listing them for this reason. Alternatively, for some groups such as nemerteans all genera are characterized. Characterization of groups only rarely includes an explicit statement of those suites of characters which are diagnostic. In some articles taxonomic characterization is presented in a manner which can be readily understood by a biologist with broad general training; but in many articles it is couched in language known only to specialists. For example, under Architectonicidae in the gastropod section (vol. 1, p. 977) appears: "The protoconch is anastropic and hyperstrophic and sharply demarcated from the ultradextral teleconch." A few of these terms may be familiar to the nonspecialist but none are found in the gastropod introductory discussion of terms and labeled diagrams. The number of illustrations varies from 58 for tardigrades, represented by about 250 species, to none for a number of much larger groups such as myriapods with 13 000 species. A more careful selection, labeling and keying of illustrations to the text could have made a number of taxonomic characterizations more intelligible to the nonspecialist.

With some exceptions the classification scheme employed in each article is in general use. Relatively few authors indicated that other schemes are also in use and the nonspecialist might assume that the nomenclature is stable whereas for many groups this is not the case. Where alternative schemes or groups are given in the text, they are sometimes not indexed. For example, Cetacea is indexed only for whale parasites and Pinnipedia is not indexed at all. Most users would probably think to look up red algae under Rhodophycota after failing to find Rhodophyta. They might be briefly put off after finding an asterisk after Phaeophyceae, which is meant to denote that the group is not treated further, a mistake in this case. A summary of the classification down to family level is given separately and concisely in an appendix to volume 2.

Habitats, biogeographic distribution, and number of described members are also often included for each higher taxon. Occasional errors are bothersome in articles which will be regarded as authoritative. In the hemichordate article it is stated that Planctosphaeroidea are represented only by specimens found in the Bay of Biscay. According to Scheltema (*Marine Biology* 7: 47–48. 1970), these specimens were not taken in the Bay of Biscay but some 350 nautical miles west of the Canary Islands; and the species has been recorded six additional times in the north Atlantic. At the level of a class the perpetuation of such errors is unfortunate. In the article on Chondrichthyes it is stated that the hexanchid sharks are worldwide in tropical and subtropical waters. However, many divers in western Canada can attest that at least one species occurs well into cool temperate waters.

References are given as additional sources of information, not to support specific statements. The number and quality vary, and, occasionally they are misplaced, e.g., a reference to Cephalocarida under branchiopods. In some cases they are quite inadequate. For example, only Dawydoff (*Traité de Zoologie*, 1948), Van der Horst (Bronn's *Tierreich* 1932–38), and Hyman (*The Invertebrates*, 1959) are given for hemichordates.

Overall, and with some notable exceptions, this compendium cannot be considered as a series of scholarly articles assessing the systematic status of each group; and one would not expect this to be so in a series of volumes less extensive than that of *Das Tierreich*. As such, specialists should expect little new information — again with some exceptions. For the nonspecialist these volumes provide a useful and time saving compilation of taxa. The volumes appear to be well bound, and this reviewer's copies have withstood numerous trips between ship and shore. A set should be made available in the reference libraries of those teaching, research, and consulting institutions with interests in identification and classification of living organisms.

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Tracers in the Sea. *Wallace Smith Broecker and Tsung-Hung Peng. Lamont-Doherty Geological Observatory, Columbia University, Palisades, New York 10964. 1982. 690 p.*

Tracers in the Sea, as the title suggests, is a book mostly on how geochemical and physical oceanographic processes can be studied using distributions of chemicals in the world's oceans. The book tends to emphasize large-scale ocean chemistry processes, comparing ocean basins to one another, for example, or examining differences between shallow and deep regions, or discussing exchanges between the atmosphere and ocean on a global scale rather than discussing detailed chemical reactions in seawater. It is thus a book

concerned more with the broad implications of these reactions to oceanography in general than with what might be called marine chemistry in which the chemical reactions in seawater are studied in their own right from an analytical or theoretical point of view.

Those familiar with Broecker's *Chemical Oceanography* will not be especially surprised by the content or style of this book. *Tracers in the Sea* deals with most of the material found in the earlier book, but the newer book has been updated and, as a comparison of the number of pages show (690 pages compared to 214 pages), has much more material included in it, a considerable amount of this newer material becoming available in the 10 years since the earlier book was written. In many respects the contents of *Tracers in the Sea* reflect the results obtained from the massive GEOSECS program by Broecker's Lamont group as well as others. Much of the book deals with natural processes, but a considerable emphasis is placed on how man is affecting some of the constituents of the ocean, particularly with regard to various radionuclides which can be used as tracers to illustrate oceanographic processes. A whole chapter in the book is devoted to the role of the ocean regarding the crucial question of the fossil fuel CO_2 buildup in the atmosphere, possibly the most profound global pollution problem facing mankind today because of the effect increased CO_2 levels in the atmosphere could have on the world's climate.

The style is lively and generally easy-to-read, almost conversational. This does not mean, however, that all of it is easy to follow. In many instances, the discussion appears elementary, but the reader should not be misled into thinking the arguments are anything but sophisticated and sometimes quite complex. A sense of the book's style can perhaps be obtained from chapter titles such as "How Fast Does the Mill Grind?," or "What Keeps the System in Whack?," or "The Anthropogenic Invasion," titles which almost sound as though they were meant for essays rather than for chapters in a science text book. The subtitles for these chapters, "Rates of Vertical Mixing and Sediment Accumulation," "Control Mechanisms in the Sea," and "The Movement of Water through the Oceanic Thermocline," however, put the material of the chapters into context.

The book possesses a scope and insight into chemical oceanography which would be very hard to find in any other book although it is not a text book of marine chemistry as such, and therefore is probably not suitable as the sole text book for a course in chemical oceanography. It is an excellent pedagogical book, often illustrating concepts by omitting some complicating features of the real ocean, then including these features or explaining what might be expected under real conditions. The body of the text does not contain many references, but there is a quite complete and useful annotated list of over 700 up-to-date references organized by topic at the end of the book. Thought-provoking problems are appended to the chapters. The methods of production, though perhaps not ideal, keep the cost of this lengthy book admirably low.

In summary, I believe *Tracers in the Sea* is a very worthwhile text book with a unique approach to chemical oceanography. It covers a wide range of material not available in any other book, and is an excellent guide to the sensible use of measurements of chemical constituents of the ocean. All chemical oceanography students and probably all students in other fields of oceanography should be familiar with it.

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Microbial Diseases of Fish. *Edited by R. J. Roberts, Special Publication No. 9 of the Society for General Microbiology. Academic Press, London. 1982. 305 p. $40.50 (U.S.)*

A Symposium of the Pathogenicity Group of the Society for General Microbiology was held at Edinburgh, Scotland, 17 September 1981. The resulting volume edited by the Symposium organizer R. J. Roberts, University of Stirling, Scotland, consists of 12 review papers by 15 contributors. It contains up-to-date information on diseases of fish and shellfish caused by viruses, bacteria, fungi, and fungi-like organisms, and information on the theoretical and practical aspects of fish immunology. Because new and practical methods of fish immunization need to be developed, this important topic is also covered.

In his paper A. E. Ellis outlines current thoughts on kinetics of the immune response in teleost fish. M. H. Manning, M. F. Grace, and E. J. Secombes review the developmental aspects of immunity and tolerance in fish. P. D. Ward deals with development of bacterial vaccines, and C. Michel presents progress toward furunculosis vaccination. According to C. Michel, the use of vaccines prepared from killed bacterial cells has severe limitations in controlling fish furunculosis. Immunization against furunculosis, however, is still in the stage of intensive investigations.

There are three papers on fish viruses begining with a keynote paper by Ken Wolf on newly discovered viruses and virus diseases of fish described between 1977–1981. B. J. Hill deals with infectious pancreatic necrosis (IPN) virus and its virulence. His coverage of the topic is detailed and broad. C. Agius discusses important viral diseases of warm water fish as well as the cell lines most suitable for their study.

The pathogenesis, or pathogenicity, of certain gram-negative bacteria is discussed in two articles. A. L. Munro deals with routes and mechanisms of infection. M. R. Horne discusses the nature of the pathogenesis of *Vibrio anguillarum* and closely related vibrios. He outlines the need to know the molecular mechanisms of the relationship between the pathogen and the host so that control of these diseases will be more effective.

More than one-third of the book deals with fungi as pathogens of fish and shellfish. D. J. Alderman deals with isolation and pathogenicity. Included also are taxonomy, host range, description of the disease, and the determination of the pathogenicity of fungi to freshwater and marine fish and shellfish. It would have helped readers, who are not mycologists, to have had a table with a review of the taxonomy and the host range of the fungi pathogenic to aquatic animals. A. H. McVicar deals chiefly with ichthyophoniasis of marine fishes: herring, plaice, and haddock. *Saprolegnia* infections in salmonid fish and their ova are common as indicated by

A. D. Pickering and L. G. Willoughby. Five other genera of Oomycetes are also pathogenic and in routine diagnosis often misidentified as *Saprolegnia*. High intensity of fungal infestation of incubating fish ova and the methods of control of saprolognios by chemical agents, however, are not discussed in this review.

Without lengthy review of each contribution, it must suffice to say that *Microbial Diseases of Fish* is an important and up-to-date contribution to fish pathology. Reading this symposium will save countless hours for interested persons who, otherwise, would need to collect and read hundreds of pertinent references. This symposium is well written and edited. Numerous good illustrations and a detailed index greatly enhance its value.

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Acid Rain. *Robert H. Boyle and R. Alexander Boyle. Nick Lyons Books, Schocken Books, New York, NY. 1983. 146 p. $8.95 (U.S.) paperback; $14.95 (U.S.) hardback.*

This is a well written, yet decidedly biased account of the "chemical leprosy eating into the face of North America." The book provides a concise, candid overview of the acid rain issue, with equal emphasis on the nature of impacts, socio-economic implications and political repercussions. It should be useful in the hands of teachers, administrators, and politicians. As well, I can recommend it to the general public, in appreciation of its very suitable style. (Robert Boyle is a long-time senior writer for *Sports Illustrated*.)

The authors effectively describe many important technical concepts, for example, interactions among atmospheric pollutants, mobilization of metals at reduced pH levels, and the deceleration of decomposition and remineralization at low pH. Much of the technical information is given in a historical context, in reference to the studies of Gorham, Likens, Bormann, Galloway, Cowling, Webster, Scofield, Harvey, and others in North America and Ericksson, Rossby, Oden, and others in Europe. The scientific story starts with Robert Angus Smith's 1872 book, *Air and Rain*, which implicated coal burning with acidified rain in the United Kingdom.

Much of the book describes impacts on aquatic and forest ecosystems, but the authors deal also with the effects of sulphate aerosols and metals leached from plumbing systems on human health, the degradation of buildings and works of art, modification of local climates and possible leaching of pollutants from landfills. The documentation of damages is thorough and convincing, although the authors point out that "no one has so far actually traced acid precipitation falling on Lake X in Maine or Lake Y in Quebec to Power Plant Z in Ohio."

The authors strike a responsive chord in professional ecologists as they question the presumptuous strategy of the liming advocates (and, implicitly, the quick fix naivity of many environmental protection agencies) who propose to "play God" and start natural ecosystems over again. As well, they support the proposition that extinction of species by pollution of natural systems is a moral issue.

The schism over environmental protection policy between government and public in the United States is illustrated through two revealing quotations. On one hand, Louis Harris, the pollster, testified before the House Subcommittee on Health and the Environment that "by 80 to 17 percent, a sizeable majority of the public does not want to see any relaxation in existing federal regulation of air pollution," one of the clearest, most overwhelming messages from the public in 25 years of surveying public opinion. On the other hand, an Environmental Protection Agency official describes the "incredible double standard working in the agency." "For those areas where the administration already knows what it wants to do, it requires no scientific proof. It goes out and looks for a preponderance of evidence, but if the preponderance of evidence indicates that regulations are required where the administration does not want to apply them, scientists are asked to come up with absolute proof of their findings." Whereas the Reagan administration "is out to gut the Clean Air Act," the National Commission on Air Quality reported that a two percent surcharge on the average utility bill in the east would bring in enough money to eliminate half the sulphur dioxide in the region. There is no criticism of governments in Canada even though the Crown-owned Ontario Hydro so far has avoided installation of sulphur dioxide scrubbers at its power plants, a point we are usually reminded of by United States power interests.

I was somewhat disappointed that the authors offered little constructive criticism of the current environmental protection system. Emphasis on a regulatory approach and polluter-pays philosophy (although everyone probably pays in practice) leads to polarization and paralysis which inhibit cost-effective, timely remedial programs. In my opinion environmental protection policy needs to be rationalized in a resources planning strategy if society is to deal effectively with large scale issues. How else can we hope to test fairly the view that we can have economically priced energy *and* healthy lakes and streams.

We should add this book to the growing list of references which we are prepared to recommend to non-professionals interested in the acid rain issue.

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Electricity Generation and the Ecology of Natural Waters. *T. E. Langford. Liverpool University Press, Liverpool. 1983 $27.98. 342 p.*

Langford sought to provide an "objective reference for ecologists" "without reference to politics or public relations" and succeeded. The available compendia on aspects of electricity generation including entrainment (Schubel and Marcy 1978), entrainment and impingement (Jensen 1978, which is not used at all), thermal effects (Krenkel and Parker 1969),

and the variety of special journal issues, reviews, and overviews of hydroelectric power generation, while treating the available material reasonably well, treat the processes of power generation and consequent effects, piecemeal.

This book is introduced by a chapter on the process of electricity generation including the wastes and processes that have the potential for ecological perturbation. Air emissions are logically given minimal treatment throughout because of its current piecemeal worldwide attention.

The organization and structure of the book are excellent and the sections on effects upon physical characteristics, water chemistry and biota are easy to follow and use. Conveniently, the biological effects are treated not only by trophic level but also by the factor(s) influencing the organism. The painstaking effort that went into segregation and treatment of the diverse subject chosen is recouped by the reader's ease in following the processes and effects.

The introductory lessons in biology scattered throughout the book detract from the synthesis done by Langford who likely hoped this approach would broaden the audience. He need not have worried as the insights given warrant the attention of industry, manager, and scientist alike. Usually, the "effects" are interpreted in light of the variety of conditions that could influence the factor in question, e.g. alterations in fish growth at/near thermal discharges are the cumulative result of movement in and out of thermally altered areas, altered food distribution patterns, altered population structure, stress or enhancement to performance resulting from changes to the habitat but, periodically, the causes leading to observed effects are not made clear.

I particularly enjoyed the final chapter entitled "Legal aspects of water use in electricity generation ..." and was pleased that Langford went beyond the scope of the title into the areas he sees as requiring study and/or resolution in relation to current trends in electricity generation. At least in North America the adversary status of the electrical industry and environmental managers/researchers has hampered both understanding the ecological implications and developing the basis for minimizing perturbations. It is indeed time for a "rational approach by politicians and government departments ... to resist minority opinion often unsupported by scientific data." It is also clear that the rational approach by politicians and governments should also be translated into a practical scheme both to provide the data and implement moves to offset the supported effects. Early predictions of dire thermal consequences from electric generating have never materialized; however, an environmental price is still being paid for the generation of electricity. The debt to the environment and society can be reconciled.

In summary, a book of this nature was long overdue and the irritants of periodic lapses in critical assessment of effects, reintroductions to biology, and, at times, ponderous style are heavily overshadowed by an excellent synthesis of the process and effects of electric power generation.

JENSEN, L. D. [ed.]. 1978. Fourth National Workshop on Entrainment and Impingement. E. A. Communications, New York, NY. 424 p.

KRENKEL, P. A., AND F. L. PARKER [ed.]. 1969. Biological aspects of thermal pollution. Vanderbilt University Press, TN. 407 p.

SCHUBEL, J. R., AND B. C. MARCY [ed.]. 1978. Power plant entrainment. A biological assessment. Academic Press, New York, NY. 271 p.

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Books Received/Livres reçus

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Directory of Marine Scientists in Canada — 1983. *Anonymous. Canadian Special Publication of Fisheries and Aquatic Sciences 65. Government of Canada, Fisheries and Oceans, Ottawa 1983. 408 p. Prepared by and available free from Secretariat, Canadian Committee on Oceanography, Department of Fisheries and Oceans, 240 Sparks Street, Ottawa, Ontario K1A 0E6.* This Directory is an inventory of marine scientists and engineers in governmental organizations, universities, and industry who are engaged primarily in research and development and consulting. It also includes scientists engaged in scientific services and management. Listed are specialties and activities of each scientist. [R506]

Opisthobranchia des Mittelmeeres: Nudibranchia and Saccoglossa. *L. Schmekel and A. Portmann. Illustrated with drawings of Ilona Richter. Springer-Verlag, Berlin, Heidelberg, New York. 1982. 410 p. ca $162.70 (U.S.); 390 DM. Fauna e Flora del Golfo di Napoli 40. (mainly in German).* This volume on part of the opisthobranch gastropods (molluscs) is the latest in the series of the fauna and flora of the Gulf of Naples, all monographs of the zoological station at Naples. It deals with the shell-less nudibranchs, detailing the taxonomy of the group and giving descriptions of the Mediterranean species in both German and English. There are rich and copious illustrations. [R507]

Canadian Tidal Manual. *Prepared by Warren D. Forrester. Department of Fisheries and Oceans, Canadian Hydrographic Service, Ottawa, Ontario 1983. 138 p. $20 (Canada), $24 (other countries).* The material in this manual was designed to provide the theoretical background and technical instruction necessary for the effective performance of the tasks involved in gathering and using tide, current, and water level information on hydrograhic field surveys. The emphasis is mainly on principles, with reference to manuals or other documentation for the specifics of particular instruments or routines. [R509]

Handbook of Tropical Aquarium Fishes. *Dr. Herbert R. Axelrod and Dr. Leonard P. Schultz. T.F.H. Publications, Inc. Neptune, New Jersey. 1983. 736 p. including 541 black and white photos, 50 color photos and 11 line drawings. $8.95 (U.S.), hard cover.* This revised edition is a practical and profusely illustrated compendium of over 425 popular aquarium fish. Included are special sections on the aquarium and its management, aquarium plants, and diseases of fishes. It is an excellent introductory guide for the beginning hobbyist. [R510]

Identification of Larval Fishes of the Great Lakes Basin with Emphasis on the Lake Michigan Drainage. *Nancy A. Auer, editor. Special publication 82-3, Great Lakes Fishery Commission, Ann Arbor, Michigan. 1982. 744 p., >200 figures. $10.50 (U.S.), $12.50 (Can.). Distributed (wrapped in plastic) as three-hole punched pages ready for insertion into a binder.* This atlas combines exiting literature with original work and illustrations of 148 species, many previously undescribed. In addition to a key to the families, accounts include diagnostic characters, meristics, and descriptions of ecology and reproductive biology of adults. Descriptions of eggs are given as are morphometric, morphological, and pigmentation characteristics of yolk-sac larvae, larvae, and juveniles. [R511]

A Guide to Integrated Fish Health Management in the Great Lakes Basin. *Fred P. Meyer, James W. Warren, and Timothy G. Carey, editors. Special Publication 83-2, Great Lakes Fishery Commission, Ann Arbor, Michigan. 1983. 272 p.* This compendium is an integrated structured guide to the implementation of fish health programs at all operational levels in the Great Lakes basin and elsewhere. The six sections are entitled, The Fish Health Management Problem, Disease Control Options in Hatchery Management, Administrative Options in Disease Control, Integrating Fish Health Management Options, Important Diseases of Salmonid Fishes, and Appendices and Glossary. Information is included on important factors that contribute to the introduction and dissemination of fish diseases, and the measures available to reduce the risks of disease exposure. [R512]

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

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